The distribution of epiphytes over environmental and habitat gradients in tropical and subtropical Australia

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Declaration of Originality

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Statement of Co-Authorship and Thesis Contributions

This thesis comprises a series of manuscripts (chapters) prepared for publication. For the purpose of this thesis references have been collated. The following person contributed to the manuscripts prepared as part of this thesis:

Prof. James B. Kirkpatrick, Discipline of Geography, School of Land and Food, University of Tasmania, Tasmania, Australia

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Author details and their contributions:

Jennifer Sanger was the primary investigator, contributed to ideas, designed the study, performed all field and laboratory work, performed all data analyses and wrote all manuscripts.

James Kirkpatrick contributed to the study design, ideas and edited manuscripts for all chapters.

The undersigned agree with the above stated “proportion of work undertaken” for each of the above published peer-reviewed manuscripts contributing to this thesis:

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Abstract

Epiphytes, plants which grow on other plants for support yet are not parasitic to their host, are a prominent feature in Australia's rainforest. Despite this, very few epiphyte studies have been undertaken in Australia. This thesis examines the distribution of vascular and non-vascular epiphytes over two spatial scales, within the host tree and across elevation, and examines how gradients of light and moisture affect these distributions. This study focuses on the two epiphyte 'hotspots' in Australia, the tropical rainforests in the Wet Tropics Region (Far North Queensland) and the subtropical 'Gondwana Rainforests' (northern New South Wales). This thesis explores how the distribution patterns found in these two Australian ecosystems compares to those found for rainforest elsewhere in the world, with special reference to epiphyte distributions over continuous light and moisture gradients and broader zonation systems.

Very little research examines the distributions of both moss and vascular epiphytes within the same study. In the subtropical site, vascular epiphytes and mosses were recorded from four height zones across five elevations between 300 and 1100 m above sea level (asl). Vascular epiphyte species richness was highest in the inner canopy (6.3 species), while mosses tended to have a uniform distribution over the height zones (3.8 - 5.0 species). Both moss and vascular epiphyte species richness peaked at mid-elevations (500 - 700 m), with moss richness peaking at a slightly higher elevation than the vascular epiphytes. Host tree characteristics (bark roughness, host size) explained very little of the species composition or richness of epiphytes. The strong patterns found in the species richness and composition of epiphytes over host tree and elevation gradients suggest that moisture, temperature and light may be one of the major influences on epiphyte distributions in this ecosystem.

Moving beyond broad zonation systems, in the tropical rainforest site, the distribution of vascular epiphytes was examined over continuous gradients of light and humidity, using individual environmental measurements for each epiphyte surveyed. There was a strong partitioning of taxonomic groups over the light and vapour pressure deficit (VPD) gradient. Orchids had the highest average total transmitted light levels and VPD (27% and 0.43 KPa, respectively), followed by the ferns (21% and 0.28 KPa) and then the other angiosperms (17% and 0.2 KPa). There was also strong partitioning of species within taxonomic groups, suggesting that microclimatic factors play an important role in the realized niche spaces of epiphytes within the tropical Australian rainforest.

Epiphytes show a strong distribution of drought mitigating traits within the host tree, but few studies have examined distribution patterns of these traits over elevation gradients. We assessed

whether epiphyte species that occupy comparable realised niche spaces within host tree and landscape scale gradients have similarities in taxonomy, morphology or physiology in the sub-tropical rainforest of Australia. Vascular epiphytes with Crassulacean Acid Metabolism and other drought-mitigating morphologies were common in the groups that occupied the most xeric situations. Vascular species with little to no drought-mitigating characteristics were common in groups that occupied moister situations. Moss morphologies were less congruent with environmental conditions than vascular plant morphologies.

Broad zonation systems are often used in epiphyte research. The effectiveness of a widely used system, the Johansson zones, was tested. Vascular epiphytes were grouped by observed substrate and microclimatic attributes and assessed for correspondence to the zones. Twenty-four epiphyte species in the tropical rainforest site were agglomerated into four groups using Ward's method. Group 4 was highly distinct and included shade loving species and nomadic vines from the lower zones of the host trees. Group 3 contained species from the most exposed habitats. Group 1 had higher light levels and lower substrate thickness than Group 2, yet both groups had close to identical distributions over the Johansson zones. This suggests that groups of epiphyte species may utilise different micro-sites within the same zone. While the Johansson zones are a useful tool in epiphyte studies, finer partitioning of habitat within the host tree may be missed.

Overall, in both the tropical and subtropical rainforest sites, epiphytes exhibited predictable distributions, of both species and traits, over the host tree, elevation, light and VPD gradients. Thus, moisture and light have a major influence on epiphyte distributions in Australia. The patterns of vascular epiphyte distribution are similar to that reported in the international literature, however, moss epiphytes had distributions that were partly exceptional, perhaps due to mosses being able to inhabit small microhabitats within the host tree. Indeed, different communities of vascular epiphytes can coexist within the same zone of the tree in Australia, and perhaps more widely, due to fine scale patchiness of habitat. The conclusion that epiphyte distributions have a strong link with microclimate has important implications for their survival in the context of climate change. Much more study is needed on epiphytes in Australia, especially the bryophytes, in order to work out how to prevent biodiversity loss.

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Introduction

Epiphytes, plants which rely on other plants for mechanical support yet are not parasitic to their host, are a diverse group, representing approximately 9% of global vascular plant species (Zotz 2013a). Non-vascular epiphytes are equally as diverse, and in some forest ecosystems can outnumber vascular plant species (Jarman and Kantvilas 1995). Epiphytes are important elements in rainforest communities, as they contribute important water and nutrient inputs through cloud stripping and provide habitat for arboreal animals (Nadkarni 1986; Benzing 1990; Pounds et al. 1999). There is extensive international literature on the ecology of epiphytes, however, studies tend to focus on the hyper-diverse Neotropics, where epiphytes can represent up to 50% of vascular plant diversity in montane wet forests (Kelly et al. 2004) and 195 vascular epiphytic species have been recorded from a single tree (Catchpole and Kirkpatrick 2010). Studies of bryophytes are less common, often due to difficulties with taxonomy (Cox and Larson 1993).

1.1 Diversity patterns of epiphytes

Epiphytes differ in a number of ways from their terrestrial relatives. Having no direct contact with the ground, epiphytes rely on regular moisture inputs from fog and rainfall. As a consequence, water and fog supply have potentially the greatest influence on epiphyte distribution (Zotz and Hietz 2001; Benzing 2004; Cardelús et al. 2006; Romanski et al. 2011; Zhang et al. 2015). As a response to this limitation of moisture, many vascular epiphytes exhibit physiological and morphological characteristics which help them cope with drought. For instance, some vascular species have Crassulacean Acid Metabolism (CAM) photosynthetic pathways, which help reduce water loss through nocturnal uptake of CO_2 (Winter 1985). Others have specialised morphologies that assist with water retention, such as thickened or succulent leaves, rhizomes or specialised water storage tissue (Hietz and Briones 1998; Benzing 2004; Higgins 2004; Reyes-García et al. 2008; Zhang et al. 2015). Epiphytic bryophytes respond to drought in a different way. They are poikilohydric, which enables them to become dormant when there are low levels of moisture (Proctor 1990; Bates 1998; Sillett and Antoine 2004). Bryophytes also have a range of growth forms, which can assist in water storage by storing water in the capillary spaces between the leaves (ver Leerdam et al. 1990; Bates 1998; Hedenäs 2001; Frahm 2003; Sillett and Antoine 2004; Sporn et al. 2010).

Epiphytes also distinctly differ from terrestrial plants due to their biotic interaction with the host tree. The size, branching patterns, bark-roughness and pH of the host can influence the abundance and species richness of epiphytes (Benzing 1990; Hietz 1999; Frahm 2003; Wyse and Burns 2011). While strict host specificity is rare, some trees are better hosts for epiphytes than others (Benzing

1990; Laube and Zotz 2006; Wallace 1981; Wyse and Burns 2011). Rough-barked trees are often preferred hosts, as furrowed bark can enhance moisture holding properties and is an easy substrate for attachment (Frahm 2003; Wyse and Burns 2011). Host trees with smooth or shedding bark or trees with allelopathic chemicals often make poor hosts (Hietz 1999; Kellar et al. 2006). The size of the host tree is important, with large host trees having higher diversity due to a larger surface area and also an increase in the time for colonization as the tree gets older and larger (Benzing 1990; Burns and Dawson 2005; Male and Roberts 2005; Woods et al. 2015; Zhao et al. 2015). The leaf size and architecture of a host tree can affect diversity patterns of epiphytes by influencing light levels and wind movement (Cardelús 2007).

The epiphyte rainforest environment has distinct gradients in moisture and light. Microclimatic conditions change dramatically from the humid and shady bases of the trunk to the exposed twigs of the outer canopy, resulting in the partitioning of the tree into a highly diverse physical environment (Wallace 1983; Théry 2001; Bartels and Chen 2012). Epiphyte species often have a strong vertical distribution within the host tree as a result of these environmental gradients (Johansson 1974; ter Steege and Cornelissen 1989; Kellar et al. 2006; Romanski et al. 2011; Krömer et al. 2007; Silva et al. 2010). Generally, there is a higher diversity of epiphytes species in the inner canopy where light and moisture are at intermediate levels and conditions are more favourable to growth than at the extremes of the outer canopy and trunk (Johansson 1974; ter Steege and Cornelissen 1989; Freiberg 1996; Krömer et al. 2007; Zotz and Schultz 2008; Cach-Pérez et al. 2013).

A vertical zonation scheme created by Johansson (1974) has been the standard method for dividing host trees into habitat zones and has been used by epiphyte researchers for decades. Zone 1 is the shaded, humid section of the base of the tree, with zones moving up the host tree through to zone 5, which consists of the exposed outer branches. Johansson (1974) found that most epiphyte species within the tropical forests of West Africa have well defined distributions that are restricted to one of these zones. Other studies have found that distributions of epiphyte species are often broader, with epiphyte communities often span adjacent zones (Wallace 1981; Catchpole 2004; Zotz 2007; Woods et al. 2015). This is likely to be due to environmental gradients being more of a continuum rather than discrete units (Wallace 1981).

Landscape scale changes in abiotic factors can also influence the distributions of epiphytes. Over an elevation gradient, there are major changes in moisture and temperature (Chantanaorrapint 2010; Strong et al. 2011). There are often distinct changes in epiphyte communities with increasing elevation as a response to these gradients (Wolf 1993, 1994; Hietz and Hietz-Seifert 1995; Wolf and Flamenco 2003; Cardelús et al. 2006). Both moss and vascular epiphytes often have a peak in species

richness at mid-elevations, a pattern which is attributed to the mid-elevations having a more favourable climate for epiphyte growth and survival (Wolf 1993; Wolf and Flamenco 2003; Cardelús et al. 2006). Mid elevations often have a higher level of rainfall and fog compared to lowland forests, yet temperatures are milder than those at high elevations (Krömer et al. 2005; Wolf and Flamenco 2003; Cardelús et al. 2006).

1.2 Epiphyte research in Australia

Compared to the highly diverse Neotropics, Australia has a modest diversity of vascular epiphytes, with an early estimate of c. 380 species (Wallace 1981). Australia possibly has a higher richness of epiphytic bryophytes, with 1847 known bryophyte species, however many species still remain undescribed (Pócs and Streimann 2006; Chapman 2009). Lack of suitable habitat may be the main reason why Australia has a low diversity of vascular epiphytes compared to other regions of the world. Usually confined to moist tropical forests, vascular epiphytes are restricted to a very small proportion of the continent. Two epiphyte hotspots have been identified within Australia (Wallace 1981): the Wet Tropics Region, a 12,000 km^2 World Heritage Listed area which covers only 0.26 % of the continent; and the subtropical rainforests, the 'Gondwana Rainforests', another World Heritage Listed area which consists of a mere 3665 km^2 (ANU 2009). Bryophytes, in comparison, have a wide distribution within Australia's rainforest ecosystems, ranging from the tropics through to the temperate zone. The cool temperate rainforests of Tasmania have a high species richness of mosses and liverworts, outnumbering vascular plant species in a ratio of 3.5 to 1 (Jarman and Kantvilas 1995). The Australian tropics and subtropics are also highly diverse, however very little is known about the number of species and their distributions (Streimann 1994; Pócs and Streimann 2006).

Orchids and ferns are equally represented among Australian epiphytes. Ferns constitute c. 40% of Australia's epiphyte diversity, while globally they account for as little as 10% (Zotz 2013a). In contrast, orchids make up c. 40% of Australia's epiphyte diversity, yet they account for 68% of vascular epiphyte species worldwide (Gentry and Dodson 1987; Zotz 2013a). Some notable epiphyte families, such as Bromeliaceae, Cactaceae, Marcgraviaceae, Cyclanthacae and Gesneriacae do not occur in Australia as they are restricted to the Neotropics (Madison 1977). Vascular epiphytes have low levels of endemism in Australia, with only eight endemic genera and no endemic families (Wallace 1981). This contrasts with Australia's terrestrial rainforest plants, as the Wet Tropics Region is second only to New Caledonia in the number of local endemic rainforest plant genera per unit area (ANU 2009).

Despite epiphytes being a prominent feature of Australia's rainforests, few comprehensive studies have been done on this charismatic group of plants. Only one study has examined the community

ecology of vascular epiphytes across different forest types (Wallace 1981). Other studies do exist, however are limited to one to four species (Male and Roberts 2005; Cummings et al. 2006; Freiberg and Turton 2007), or focus on plant physiology, including photosynthetic pathways (Winter et al. 1983, 1986) and nitrogen utilization (Bergstrom and Tweedie 1998). Studies on Australia's tropical and subtropical epiphytic bryophytes are also few (Fensham and Streimann 1997; Franks and Bergstrom 2000; Ramsay and Cairns 2004). This lack of study into a key group of Australia's tropical and subtropical rainforest plants allows for many potential research questions. While there is extensive literature on the distribution of epiphytes, how do the patterns described in the international literature compare to those in Australia? Australia has many differences in epiphyte flora compared the rest of the world: a lower abundance and diversity of vascular epiphytes, substantial differences in species composition and relatively small, isolated and fragmented pockets of suitable epiphyte habitat. These factors may lead to different distribution patterns to those found in other parts of the world.

Many studies on epiphytes have focused on the distribution of epiphytes either within the host tree or across an elevation gradient (ter Steege and Cornelissen 1989; Wolf 1993, 1994; Wolf and Flamenco 2003; Cardelús et al. 2006; Krömer et al. 2007; Zotz and Schultz 2008; Silva et al. 2010), however research that encompasses both gradients is rare. Australia's low abundance of vascular epiphytes is advantageous in this regard as landscape scale epiphyte studies can be easily implemented in Australia's rainforest due to the lower time required to survey individual host trees. Furthermore, this comparatively lower level of abundance reduces inter species interactions such as competition or facilitation between individuals, therefore lessening the likelihood of confounding factors.

Some gaps in the international literature do exist. There is little published on epiphytic bryophytes, especially studies which focus on subtropical or tropical regions (Cox and Larson 1993). Cryptogams can make up a substantial proportion of overall diversity (Cox and Larson 1993; Wolf 1994; Jarman and Kantvilas 1995), however bryophytes are often neglected in tropical surveys because of difficulties with taxonomy (Cox and Larson 1993) or are surveyed without including vascular plants (e.g. Romanski et al. 2011). Studies which include both vascular and non-vascular epiphytes are rare (Wolf 1994, Kelly et al. 2004). Furthermore, bryophyte studies in Australia are generally limited to the lower trunk of the host tree (eg. Franks and Bergstrom 2000; Kellar et al. 2006). This limitation means that approximately half of the bryophytic epiphyte species, those confined to the crown, are not recorded (Sporn et al. 2010).

1.3 The focus of this thesis

This thesis determines how Australia's subtropical and tropical epiphytes vary in response to two environmental gradients: within the host tree and across elevation. The thesis will compare the ecological relationships of Australian rainforest epiphytes to those established in other parts of the world. The study areas include the two important epiphyte 'hotspots' (Wallace 1981): the tropical rainforests of the Wet Tropics Region in Far North Queensland (Mt Lewis, 60 km north-west of Cairns) and the subtropical 'Gondwana Rainforests' of northern New South Wales (Border Ranges National Park, 100 km south of Brisbane).

Chapter 2 examines the general distribution patterns of vascular and moss epiphytes within the subtropical rainforest environment. This chapter looks at diversity patterns over broad zones within the host tree and over an elevation gradient, which represent gradients of light and moisture. Other aspects influencing epiphyte composition, such as bark type are taken into account. This chapter, published in *Australian Journal of Botany* in 2015, is the first comprehensive study published detailing the community composition and distribution of epiphytes in Australia. It is also one of the few papers globally to evaluate both vascular and moss epiphytes together.

Chapter 3 goes beyond the broad zones used in the study in Chapter 2 and examines vascular epiphyte distributions at a finer scale, specifically looking at how vascular epiphytes distributed over continuous gradients of light and moisture. Focusing on the Wet Tropics rainforest, environmental data was collected for individual epiphytes to evaluate how taxonomic groups of epiphytes, and species within and between groups, respond to gradients of light and moisture.

Chapter 4 details the distribution of morphological and physiological characteristics of vascular and moss epiphytes within Australia's subtropical rainforests. This study examines distributions over two scales: within the host tree and across an elevation gradient. Many studies which describe the distributions of epiphyte morphologies and physiologies are restricted to within the host tree and do not incorporate landscape scale gradients. Furthermore, this paper combines vascular and moss epiphytes, examining the differences between the two groups.

Chapter 5, which has been published in *Biotropica* in 2016, evaluates the use of the Johansson zones, a commonly utilised system for describing the vertical distribution of epiphytes. The distributions of vascular epiphytes from the Wet Tropics Region are used to test how well these groups fit with the Johansson zones.

In Chapter 6, an overall assessment of the environmental influences on epiphytes in Australian rainforest is made and the patterns are compared to those revealed for rainforests in the other parts

of the world. This conclusion discusses further areas of research and the possible impact of climate change on Australia's epiphyte populations.

The substantive chapters are written as stand-alone papers, that are published or in the process of submission for publication.

Chapter 2

Moss and vascular epiphyte distributions over host tree and elevation gradients in Australian subtropical rainforest

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2.1 Abstract

There is a lack of comprehensive studies on the ecology of epiphytic flora in Australia's rainforests. Globally, rainforest epiphyte distribution is determined by three main factors: microclimate within the host tree, landscape changes in macro-climate and the characteristics of the host tree. We test the influence of these factors on the species richness and composition of vascular and non-vascular epiphytes in the subtropical rainforest of the Border Ranges in New South Wales. Vascular epiphytes and mosses were recorded in-situ from four height zones, with ten trees sampled at five elevations between 300 and 1100 m above sea level (asl). Vascular epiphyte species richness was highest in the inner canopy (6.3 species), while mosses tended to have a uniform distribution over the height zones (3.8 - 5.0 species). We found that both moss and vascular epiphyte species richness peaked at mid-elevations (500 – 700 m), with moss richness at a slightly higher elevation than the vascular epiphytes. Host tree characteristics (bark roughness, host size) explained very little of the species composition or richness of epiphytes. Strong patterns in species richness and composition over host tree and elevation gradients suggest that moisture, temperature and light may be the major influences on epiphyte distributions in the Border Ranges.

2.2 Introduction

Vascular and non-vascular epiphytes are prominent in Australia's subtropical forests, especially over mid to upper elevations where humidity is high (Webb 1968; Wallace 1981). Australia has approximately 400 vascular epiphyte species (Wallace 1981). The Australian tropics and subtropics have large numbers of epiphytic moss species, but many remain undescribed and their distributions are poorly known (Streimann 1994; Pócs and Streimann 2006). Our knowledge of the ecology of Australian rainforest vascular epiphytes is limited to a pioneering study of the community ecology of vascular epiphytes across different forest types (Wallace 1981), a comparative study of four species (Cummings et al. 2006) and a study of one species (Freiberg and Turton 2007). The few other examples in the literature focus on plant physiology, including photosynthetic pathways (Winter et al. 1983, 1986) and nitrogen utilization (Bergstrom and Tweedie 1998). Studies on Australia's tropical

and subtropical epiphytic bryophytes are also few (Fensham and Streimann 1997; Franks and Bergstrom 2000; Ramsay and Cairns 2004) and are largely limited to the lower trunk of the host. This limitation means that approximately half of the bryophytic epiphyte species, those confined to the crown, are not recorded (Sporn et al. 2010).

Host trees represent a strong gradient of light and humidity, from the exposed outer crown to the moist, shaded base (Wallace 1981; Bartels and Chen 2012; Théry 2001). As a result, epiphyte species' distributions are partitioned over different microclimatic ranges within the host tree (vascular plants e.g.: ter Steege and Cornelissen 1989; Krömer et al. 2007; Zotz and Schultz 2008; Bryophyta e.g.: Silva et al. 2010; Romanski et al. 2011). The landscape scale is also important, as rainfall, humidity and temperature levels can vary with elevation. Montane environments are often shrouded in cloud cover, resulting in high levels of humidity and rainfall (Chantanaorrapint 2010; Strong et al. 2011). Furthermore, temperature decreases with increasing elevation (Strong et al. 2011). Epiphytes, along with terrestrial species, exhibit strong changes in species richness and composition with elevation (Wolf 1993, 1994; Hietz and Hietz-Seifert 1995; Wolf and Flamenco 2003; Cardelús et al. 2006).

Host tree characteristics can further influence vascular and non-vascular epiphyte distributions. While strict host specificity is rare, some trees are better hosts for epiphytes than others (Wallace 1981; Benzing 1990; Laube and Zotz 2006; Wyse and Burns 2011). Bark type can affect epiphyte diversity, as properties such as moisture retention, pH and shedding characteristics can vary between tree species (Hietz 1999; Benzing 2004; Sillett and Antoine 2004). The height, architecture and leaf size of trees can influence epiphyte diversity by influencing light levels (Cardelús 2007).

Many studies in other regions of the world have found that vascular and non-vascular epiphyte species richness and composition responds to either environmental variation within the host tree or elevation gradients (ter Steege and Cornelissen 1989; Wolf 1993, 1994; Wolf and Flamenco 2003; Cardelús et al. 2006; Krömer et al. 2007; Zotz and Schultz 2008; Silva et al. 2010). Research that encompasses both gradients is rare, as is the inclusion of both vascular and non-vascular epiphytes (Wolf 1994). Cryptogams can make up a substantial proportion of overall diversity (Cox and Larson 1993; Wolf 1994; Jarman and Kantvilas 1995), however, bryophytes are often neglected in tropical surveys because of difficulties with taxonomy (Cox and Larson 1993) or are surveyed without including vascular plants (e.g. Romanski et al. 2011).

The present paper, to the authors' knowledge, is the first to compare the distribution patterns of vascular and moss epiphytes over both elevational and within tree gradients in Australia. Specifically,

we ask the following questions: 1) How does species richness and composition of vascular and moss epiphytes vary over host tree height and elevation gradients in the subtropical rainforests of Australia? 2) How do these species richness and species composition patterns correlate with host tree characteristics and environmental factors such as light?

2.3 Materials and Methods

2.3.1 Study Area

The study was conducted in the Border Ranges National Park (28°21'35"S, 152°59'10"E), in northern New South Wales, Australia. The park is a World Heritage listed area of subtropical rainforest that ranges in elevation from 200 - 1100 m asl, covering a total of 3,600 km^2. These forests are a biological 'hotspot' as they are in the transition zone between the tropical north and the temperate forest of the south (Burbidge 1960). Warm subtropical complex notophyll vine forest occur in the lower elevations of the Border Ranges National Park (< 600 m asl), grading into cool subtropical complex notophyll vine forest (600 - 1000 m asl) and to simple microphyll fern forest or 'cool temperate' cloud forests above 1000 m asl (Laidlaw et al. 2011). A set of long term, altitudinal monitoring plots of the IBISCA model (Kitching et al. 2011) have been established on the western side of the reserve.

While there are no detailed climate data available for our Border Ranges plots, data are available in the nearby IBISCA transect in Lamington National Park (approximately 20 km north-east of the Border Ranges transect). In the Lamington transect, there is a strong gradient of temperature and humidity changes with increase in elevation (Strong et al. 2011). The average annual temperature decreases by 0.75 ^{o}C with every 100 m gain in elevation, with a 6-7 ^{o}C difference between 300 and 1100 m asl (Fig. 2.1a). Rainfall is on average 20% higher at upper elevations (900 m) than it is at the lower elevations (100 m). Rainfall is mildly seasonal, with 30% of rainfall falling between February and March. August and September are the driest months, receiving 7% of the average annual rainfall. During the drier months, daytime relative humidity increases with elevation (Fig. 2.1b). There is little difference in humidity during the wet season, with humidity levels at close to 100% throughout the day. The cloud base normally settles at around 700 m. Maximum daytime temperatures are higher and daytime humidity levels are generally lower in the canopy compared to the understorey of the forest.

2.3.2 Epiphyte Distributions

Five sites were chosen on the western side of the reserve. Sites were based on elevation, occurring at 200 m intervals ranging from 300 to 1100 m. At each site, ten large trees were selected for their suitability for climbing. Suitable trees were ones that had no obvious signs of rot or decay, had large, sturdy branches within 25 m of the ground and were unobstructed by vines. Trees were climbed using single and double rope arborist techniques (Lowman and Moffett 1993). For each host tree, the species, height, tree diameter at breast height (DBH), bark roughness (visually assessed; ranked on roughness from 1 to 3) and the exact elevation and location (x-y coordinates) were recorded. At some sites, suitable climbing trees were difficult to find (mostly due to high levels of vines in the inner canopy), so gaining equal replication of host tree species or even bark type was unachievable. Fifteen tree species and ten families of trees were sampled (Table 2.1). Field work was conducted between May and July 2013.

Four height zones were surveyed in each host tree, adapted from the zonation system used by Johansson (1974): inner canopy (the inner third of the branches in the crown), the upper trunk (the mid-point of the trunk to the first bifurcation) the lower trunk (two metres above the base of the trunk to the mid-point of the trunk) and the base (from the ground to 2 m). The outer and mid canopies were not surveyed as they are usually difficult to safely access.

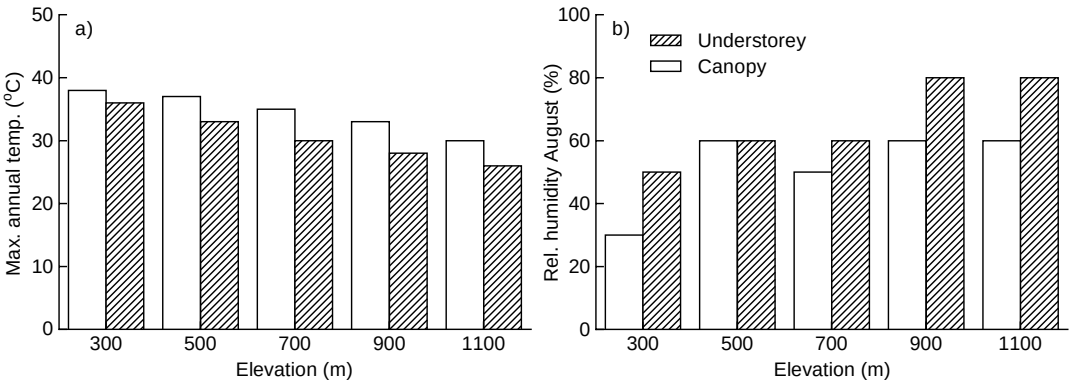

Fig. 2.1: Average maximum annual temperature (a) and average relative humidity at midday at the driest month of the year (b; August) across the five elevations on the IBISCA transect at Lamington National Park, located 20 km from the Border Ranges. Both graphs are adapted from Strong et al. (2011).

Table 2.1: A list of the host trees surveyed for epiphytes in the Border Ranges National Park. The table shows the tree species name, family, bark roughness (Bark) and the number of each species sampled over the five elevations.

Host tree species	Family	Bark	300 m	500 m	700 m	900 m	1100m
Acronychia octandra (F.Muell.) T.G.Hartley	Rutaceae	1	-	-	1	-	-
Acronychia pubescens (F.M.Bailey) C.T.White	Rutaceae	1	-	-	2	2	2
Argyrodendron actinophyllum (F.M.Bailey) Edlin	Malvaceae	2	1	3	-	3	-
Argyrodendron trifoliolatum F.Muell.	Malvaceae	2	-	2	1	-	-
Brachychiton acerifolius (A.Cunn. ex G.Don) F.Muell.	Malvaceae	1	1	-	-	-	-
Cryptocarya erythroxylon Maiden & Betche	Lauraceae	1	1	-	1	1	-
Diploglottis australis (G.Don) Radlk.	Sapindaceae	1	1	-	-	-	-
Elaeocarpus grandis F.Muell.	Elaeocarpaceae	1	2	-	-	-	-
Euroschinus falcatus Hook.f.	Anacardiaceae	1	2	-	-	-	-
Ficus watkinsiana F.M.Bailey	Moraceae	1	-	-	1	-	-
Geissois benthamiana F.Muell.	Cunoniaceae	1	1	1	4	1	3
Nothofagus moorei (F.Muell.) Krasser	Nothofagaceae	3	-	-	-	-	5
Sloanea woollsii F.Muell.	Elaeocarpaceae	1	-	5	-	2	-
Toona ciliata M.Roem.	Meliaceae	2	1	-	-	-	-

In the height zone of each tree, the number of each species of vascular epiphytes was recorded. Both holo-epiphytes ('true' epiphytes), hemi-epiphytes (epiphytes that spend part of their life cycle attached to the ground) and semi-epiphytic climbers were included in the survey. Semi-epiphytic climbers, such as species belonging to the genera *Microsorum*, *Arthropteris* and *Pothos*, are functionally similar to hemi-epiphytes, as their adventitious roots are often used for nutrient and water uptake and they will occasionally lose their connection to the ground (Wallace 1981). Clumped plants or creeping species were counted as one individual, similar to the methods used by Sanford (1967). Specimens that could not be identified in the field were collected and taken to the Queensland Herbarium (BRI) for identification. Species names used in the present paper are the accepted scientific names according to the Australian Plant Census (Council of Heads of Australasian Herbaria 2015) and the Australian Orchid Name Index (Clements and Jones 2008).

Non-vascular epiphytes were surveyed by collecting samples from each height zone of the host tree. Any mosses that appeared to be different species were collected in each height zone of a tree, with approximately 15 minutes spent collecting in each zone. Samples were taken to the Queensland Herbarium for sorting at a later date. Due to the large number of trees sampled and the limited time spent on each tree, it is highly possible that bryophyte species richness was underestimated. However, we focused on mosses, rather than the more cryptic hepatics, to reduce the likelihood of

missing rare or inconspicuous species. The samples were sorted into morphospecies and were identified to either genus or species level where possible. Nomenclature follows the AusMoss database (Klagenza et al. 2015).

Hemispherical canopy photography was used to estimate transmitted light. This method is widely used to record the canopy structure, and to calculate light transmission and exposure of a particular point within a forest (Frazer et al. 1999). A Cannon 5D mark III digital camera (Ohta-ku, Tokyo, Japan) with a Rokinon 8mm f/3.5 HD Fisheye Lens (Gangnamgu, Seoul, Korea) was used to take hemispherical photos. Photos were taken within each height zone, with three to five photos taken on both the north and south side of the tree. Photos were analysed using Gap Light Analyser (Frazer et al. 1999) which calculates the percentage of total transmitted light for each image over an entire year. This is achieved by transforming the image pixel positions into angular coordinates (Frazer et al. 1999). Hemispherical canopy photography is best conducted under uniformly overcast conditions to remove the effect of direct solar irradiance. Due to our limited time in the field, we were unable to take photos only on overcast days. To account for this, all photos were taken in manual mode with adjusted aperture and shutter speed to best suit light conditions. Prior to analysis in Gap Light Analyser, photos were edited in Photoshop (Adobe, San Jose, CA, USA) in which light was balanced using a standardised histogram reference and clarity and edge sharpness was increased to help reduce highlights from around the edge of leaves.

2.3.3 Data analysis

Differences in vascular epiphyte richness and moss richness were tested over the elevation and height zone classes using general linear models (GLM), with total transmitted light, bark roughness and host tree height and DBH added to the models as covariates. A GLM model was also used to test for differences in average total transmitted light among the height zones and elevation. A one-way ANOVA was used to test how host tree height and DBH varied over the height zones and elevation. Tukey's T analysis was used to test differences in means for pairwise comparisons.

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson and ter Braak 2003) was used to examine the effects of elevation and height zone on vascular and moss epiphyte composition. PERMANOVAs were conducted on Bray-Curtis similarity matrices and were calculated on non-transformed data. For both vascular and moss epiphytes, non-metric multidimensional scaling (MDS) plots were created to visually depict differences in species composition over the height zone and elevation gradients. BEST analysis was used to test the effect of total transmitted light, bark roughness and host tree height and DBH on the species composition

of the epiphytes groups. BEST is a permutational procedure which determines the rank correlation of species and environmental similarity matrices using the Spearman rank order correlation coefficient (Clarke et al. 2008). All GLM and ANOVA's were completed in Minitab 16.1.0 (MINITAB, Pennsylvania, USA). PERMANOVA, BEST and MDS analyses were completed in Primer v.6 and PERMANOVA+ add-on software (Primer-E Ltd, Plymouth, UK).

2.4 Results

Thirty-four species of vascular epiphytes were found, including 17 species of fern, 13 species of orchid and 4 species of dicotyledonous plants. Of these, 28 were holo-epiphytes, five were semi-epiphytic climbers and one was a hemi-epiphyte. Forty-two morphospecies of moss were recorded. All but 12 moss morphospecies were identified to either genus or species level, with species occurring in 19 different families (Appendix 2).

The species richness of both vascular and moss epiphytes varied over the two gradients of height and elevation (Table 2.2). Vascular epiphyte species richness was highest in the inner canopy, with the lowest species richness on the lower trunk. Species richness of the mosses was more consistent over the height zones than the vascular epiphytes, with only the inner canopy having higher species richness than the lower trunk (Fig. 2.2a). Vascular richness was highest at 500 - 700 m in elevation, followed by 900 - 1100 m, and was lowest at 300 m. Moss species richness had a similar pattern, however richness peaked at 700 m in elevation (Fig. 2.2b). None of the environmental or host tree covariates were significant for either vascular or moss species richness (Table 2.2).

Vascular epiphyte species composition was influenced by elevation and height zone, with a significant interaction between the two terms (PERMANOVA: Pseudo-F = 3.16; P = 0.001). The vascular species composition in the inner canopy was significantly different between all pairs of elevations. A similar pattern was found for the upper trunk, excluding the 300 m site. There was little difference in the species composition of the base and lower trunks across the entire elevation gradient. All elevations were significantly different from one another except for the higher elevations (700, 900, 1100 m) in the lower zones (lower trunk and base). Generally, there is a larger difference in vascular species composition between the height zones than the elevations (Fig. 2.3a).

Table 2.2: Summary of the two-way ANOVA results for moss and vascular epiphyte richness over elevation and height zone and the co-variates: total transmitted light, bark roughness, host tree height and DBH. *F*- and *P*-values are given for the factors of elevation (df = 4), height zone (df = 3) and for the interaction for elevation and height zone (df = 12). The F-and P-values for the covariates light, bark roughness, host tree height and host tree DBH are also shown. Bold P-values denote significant ($P < 0.05$) differences.

	Vascular species richness		Moss species richness	
	F-value	*P*-value	*F*-value	*P*-value
Elevation	6.53	**< 0.001**	8.65	**< 0.001**
Height zone	33.42	**< 0.001**	3.18	**0.025**
Elevation * height zone	1.58	0.101	1.69	0.072
Covariates:				
Total transmitted light	0.15	0.701	0.13	0.721
Bark roughness	0.13	0.724	1.17	0.281
Host tree height	0.59	0.442	1.85	0.176
Host tree DBH	0.13	0.724	0.06	0.814

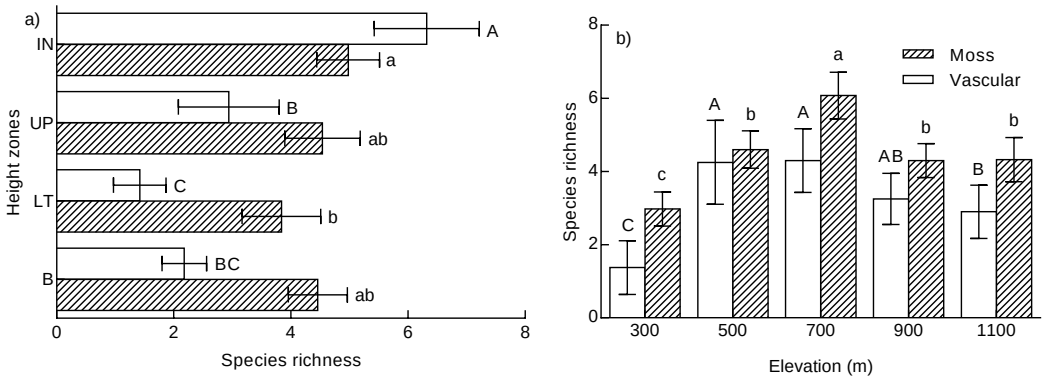

Fig. 2.2: The moss and vascular species richness (mean ± standard error) over the four height zones (a; IC = inner canopy, UT = upper trunk, LT = lower trunk, B = base) and five elevations (b). Different letters signify significant ($P < 0.05$) differences, with capital letters for the vascular species richness and lower case letters for the moss species richness.

There was a significant interaction between height zone and elevation on the species composition of the moss epiphytes (PERMANOVA: Pseudo-*F* = 1.54; *P* = 0.005). The MDS plot (Fig. 2.3b) shows some differentiation between the height zones, with the base having a significantly different species composition to the rest of the height zones, and the lower trunk different to all of the upper height zones except the 300 m site. The 900 and 1100 m sites had similar moss species compositions, with 300 m being the most significantly different elevation.

The BEST analysis showed that light was the most important factor, with total transmitted light explaining 22.1% of variation for vascular species and 16.0% for the mosses. Bark roughness

(vascular: 4.0%; moss: 1.2%), host tree height (vascular: 0%; moss: 0.8%) and host tree DBH (vascular: 2.1%; moss: 0%) had little effect on species composition.

There was a significant difference in the height of the host trees between the five elevations, with 500 and 700 m having significantly taller trees than the other elevations (ANOVA: *F*-value = 12.59; *P* < 0.001; Fig. 2.4). For the DBH of the host trees, the 900 m site had the smallest average DBH, but was only significantly different from the 1100 m site (ANOVA: *F*-value = 3.76; *P* = 0.01; Fig. 2.4).

There was a difference in the total transmitted light over the height zones, with a linear increase in light from the base up to the inner canopy (ANOVA: *F*-value = 61.1; *P* < 0.001; Fig. 2.5) There was also some minor differences in the light levels over the elevation gradient (ANOVA: *F*-value = 14.8; *P* < 0.001). Total transmitted light was highest at 1100 m, however was only significantly different to the 500 m site, which had the lowest level of light.

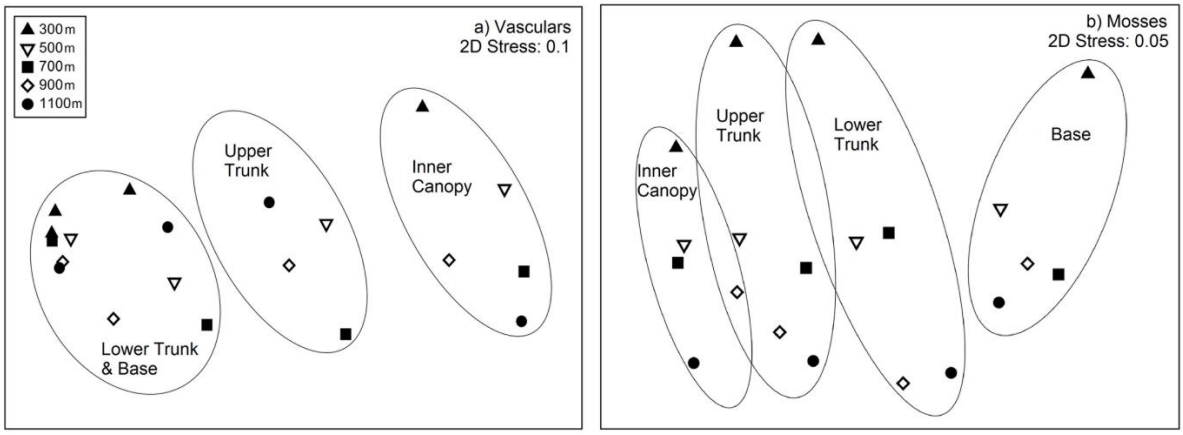

Fig. 2.3: MDS plot of the vascular (a) and moss (b) species composition for each height zone/elevation. Both plots show the two factors: elevation (as depicted by icons) and height zones (as indicated by circles).

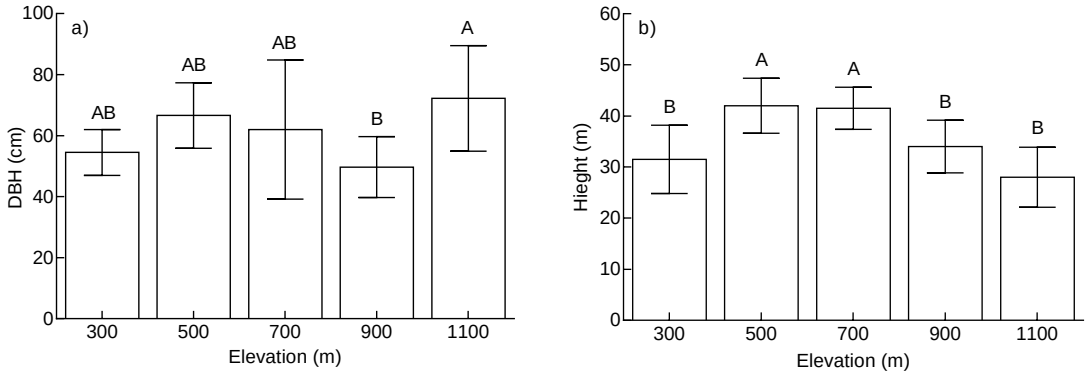

Fig. 2.4: Differences in the host tree DBH (a) and height (b; mean ± standard error) over the five elevations. Different letters signify significant differences (*P* < 0.05).

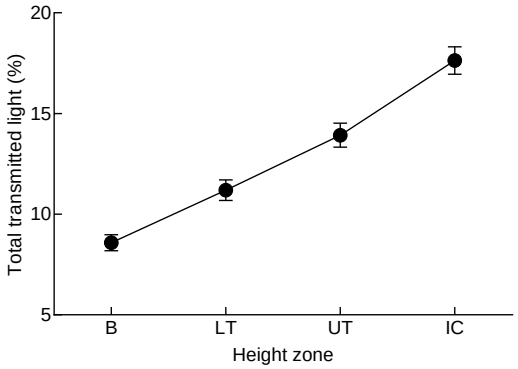

Fig. 2.5: Changes in total transmitted light (mean ± standard error) over the four height zones (IC = inner canopy, UT = upper trunk, LT = lower trunk, B = base).

2.5 Discussion

Vascular epiphytes had a comparable distribution over the host tree gradient to that observed elsewhere in the world, with the highest species richness in the inner canopy (ter Steege and Cornelissen 1989; Freiberg 1996; Krömer et al. 2007; Cach-Pérez et al. 2013). Light and humidity levels are at moderate levels in the inner canopy, which is favourable for vascular epiphytes (Benzing 1990; Krömer et al. 2007). The inner canopy also provides a wider range of microhabitats than the trunk, with forks and horizontal branches where humus and thick layers of moss can accumulate. These accumulations provide habitat for many vascular species (ter Steege and Cornelissen 1989; Benzing 2004; Krömer et al. 2007). The semi-epiphytic climbers were dominant in the base and lower trunk zones, leading to the high level of similarity in the vascular species composition in these two zones.

The mosses, in contrast to the vascular epiphytes, had fairly uniform species richness over the height gradient. This differs from other studies which found that bryophyte species richness is highest in the inner canopy (Acebey et al. 2003; Sporn et al. 2010) and/or on the upper trunk (Romanski et al. 2011; Silva and Pôrto 2013). Mosses are often divided into ‘sun’ or ‘shade’ epiphytes. A distinct vertical stratification of species composition within the host trees is common in bryophyte communities (Holz et al. 2002; Acebey et al. 2003; Romanski et al. 2011; Silva and Pôrto 2013). The distinction between sun and shade mosses is apparent in our study, as there is a large difference in species composition between the base of the host tree and the other height zones. Buttress roots can differentiate the environment at the base of the tree from the rest of the host tree, creating a shadier more humid microclimate, leading to markedly different species composition.

Both moss and vascular epiphytes showed a distinct peak in species richness at mid-elevations, which is a similar pattern to other regions of the world (Wolf 1993; Wolf and Flamenco 2003; Cardelús et al. 2006). This pattern may be attributed to the mid-elevations having a more favourable climate for epiphyte growth and survival. Mid elevations often have a higher level of rainfall and fog

compared to lowland forests, yet temperatures are milder than those at high elevations (Krömer et al. 2005; Wolf and Flamenco 2003; Cardelús et al. 2006). However this pattern may be due, in the case of the Border Ranges, to a higher rate of species loss at high and low elevations during the climatic fluctuations of the Quaternary (Bowler et al. 1976). The mid elevation peak may also be explained by the Mid-Domain Effect (MDE), which states that due to geometric boundary constraints, random placement of species ranges will produce higher species richness in the centre (Colwell and Lees 2000). Another study has shown that the MDE substantially influenced the diversity of epiphytes over an elevational transect in Central America (Cardelús et al. 2006). The slightly higher peak in moss richness compared to vascular epiphytes is a pattern found elsewhere (Benzing 1998) and may be explained by the association of mosses with cool and wet conditions (Wolf 1994; Benzing 1998; Sillett and Antoine 2004).

Other studies have examined the turnover of epiphyte species over larger elevation gradients than ours: 1550 m in Mexico (Hietz and Hietz-Seifert 1995); 1600 m in Spain (Caritat et al. 1997); 2570 m in Costa Rica (Cardelús et al. 2006); and 2420 m in the northern Andes (Wolf 1993; 1994). However, even over a 900 m gradient in the present study, we were able to find noticeable differences in the species richness and composition of epiphytes. Our 900 m gradient represented a 6-7 ^{o}C temperature difference and a 20% increase in rainfall between the 300 and 1100 m sites (Strong et al. 2011), a climatic gradient reflected in the terrestrial vegetation in this region, with distinct shifts from warm subtropical rainforest at the 300 m site through to cool temperate rainforest at 1100 m site (Laidlaw et al. 2011).

Both moss and vascular epiphytes showed strong changes in species richness and composition over elevation and height zones, which represent gradients of humidity, light and temperature. Total transmitted light, however, only explained a moderate amount of the variation in the composition of vascular epiphytes (22.1%) and moss epiphytes (16.2%). Some studies have found that light described up to 50% of the variation in composition of moss species in montane forests in Costa Rica (Holz et al. 2002), while environmental factors in the lowland forests of Panama explained as little as 10% for vascular epiphytes (Zotz and Schultz 2008). This suggests that while light does explain some of the species composition, other factors or random variation may contribute to the diversity and composition of epiphytes in our study area.

The effect of host tree species on epiphyte composition has been widely documented (ter Steege and Cornelissen 1989; Benzing 1990; Callaway et al. 2002; Zotz and Schultz 2008; Wyse and Burns 2011), yet had little influence on species richness or composition in our study area. Bark roughness had a small influence on vascular epiphytes (4%), which is largely due to the association of two

orchid species with rough barked host trees. *Tetrabaculum tetragonum* was found only on Argyrodendron sp., while *Thelychiton falcorostrus* occurs exclusively on *Nothofagus moorei*. The bark type of a host tree can vary in properties beyond roughness characteristics, such as its water retention properties, chemical composition and pH (Hietz 1999; Benzing 2004; Sillett and Antoine 2004), and it is possible that these features may influence epiphyte diversity. The size of a host tree is often influences epiphyte diversity, as large trees provide a greater surface area for epiphytes to establish on and large trees are often older, which allows for greater time for establishment (Hietz-Seifert et al. 1996; Zotz and Schultz 2008). There were differences in the size of the host trees over our elevation gradient, with the tallest trees at mid-elevations, where epiphyte species richness was the highest. Host tree had no effect on species composition in the model, however it is possible that there may have been effects from host size or other attributes of host tree architecture that were interpreted as elevation effects.

Biotic interactions may have influenced species richness and composition. Bryophytes can accumulate in thick mats, creating a deep layer of organic matter which can facilitate the colonisation by vascular epiphytes by acting as water and nutrient reservoirs (van Leerdam et al. 1990; Hietz et al. 2002). Competition has been found to strongly influence the community composition of the mosses, a factor which may have influenced moss distributions in this study (Zamfir and Goldberg 2000). It is unlikely that competition has a strong influence on the distribution of the vascular epiphyte species as they are usually in low abundance in Australian rainforests (Wallace 1981).

2.6 Conclusion

Vascular and moss epiphytes showed variation in species richness and composition over the height of the host tree and the elevation gradient, a result which is largely consistent with patterns observed elsewhere in the world. Host tree height and elevation represent strong gradients of environmental factors such as moisture, temperature and light (Wallace 1981; Théry 2001; Chantanaorrapint 2010; Strong et al. 2011; Bartels and Chen 2012). Surprisingly, host tree characteristics had little influence over the species richness or composition of epiphytes, which differs from the majority of studies conducted in rainforests outside Australia (ter Steege and Cornelissen 1989; Wolf 1993, 1994; Wolf and Flamenco 2003; Cardelús et al. 2006; Krömer et al. 2007; Zotz and Schultz 2008; Silva et al. 2010). This result suggests that environmental variables may have the strongest influence over epiphyte distributions in the Border Ranges. However, light was only able to explain a moderate amount of variation, suggesting that other factors or random variation may be influencing the species richness and composition of epiphytes in this system.

Considering the importance of elevational climate gradients on the distribution of epiphytes, climate change may severely impact on epiphyte species in Australia's montane environments. The Border Ranges region is predicted to undergo a decrease in winter rainfall and a rise in temperature which may increase the elevation at which the cloud base settles (Still et al. 1999; CSIRO and Bureau of Meteorology 2015). Species that occur in the upper elevations and mountain tops may face a reduction or complete loss of habitat (Pounds et al. 1999; Williams et. al. 2003; Costion et al. 2015). Recent distribution modelling of Australia's Wet Tropics found that the future suitable climate niche of 19 high elevation plant species would reduce by an average of 81% (Costion et. al. 2015). However, the canopy of a rainforest tree is a highly heterogeneous environment with a wide range of microclimates. Species with poor dispersal abilities may be able to occupy suitable microclimates within their current geographical ranges. Further research is needed into this topic, especially identifying which species at high elevations are at risk of habitat loss.

Chapter 3

The distribution of vascular epiphytes over gradients of light and humidity in north-east Australia

3.1 Abstract

Microclimatic conditions have a strong influence over the distribution of vascular epiphytes. Our study compares how epiphytes both within and between taxonomic groups are distributed over gradients of light and humidity. Individual total transmitted light measurements were recorded for individual epiphytes over five elevations, ranging from 800 m to 1180 m in the lower montane rainforests of north-east Australia. Data loggers recorded the vapour pressure deficit (VPD) at the forest floor and canopy of each site. There was a strong partitioning of taxonomic groups over the light and VPD gradient. Orchids had the highest light levels and VPD (27% and 0.43 KPa, respectively), followed by the ferns (21% and 0.28 KPa) and then the other angiosperms (17% and 0.2 KPa). There was also strong partitioning of species within taxonomic groups, suggesting that microclimatic factors play an important role in the realized niche spaces of epiphytes within the tropical Australian rainforest.

3.2 Introduction

One of the most studied themes in ecology relates species distributions to environmental gradients, such as temperature, moisture, nutrients and light (Barbour et al. 1980; Egan and Williams 1996; Gurevitch et al. 2002; Tateno and Takeda 2003; Engelbrecht et al. 2007). One group of plants that show distinct partitioning within the abiotic environment are epiphytes: plants that rely on other plants for support, have no direct connection to the ground and are not parasitic to their host (ter Steege and Cornelissen 1989; Krömer et al. 2007; Zotz and Schultz 2008). Within the host tree, epiphytes are subject to wide ranging gradients of light and moisture, from the exposed, high light environment of the outer canopy, through to the shady, humid base of the tree. Light and humidity often have an inverse relationship with each other and can vary dramatically from the base of the host tree to its outer branches (Wallace 1981; Théry 2001; Bartels and Chen 2012). Furthermore, landscape scale changes in elevation can affect temperature, humidity and rainfall (Chantanaorrapint 2010; Strong et al. 2011).

Water and light availability are the two environmental factors that have the biggest influence on epiphyte distributions. Scarcity of water is postulated to be the limiting factor for epiphytes (Zotz

and Hietz 2001). As a consequence, water supply, both overall and at specific times, has potentially the greatest influence on epiphyte distribution (Gentry and Dodson 1987; Zotz and Hietz 2001; Benzing 2004; Cardelús et al. 2006; Romanski et al. 2011, Zhang et al. 2015). Irradiation is also important in determining epiphyte distributions, with many epiphyte species showing distinct preference for high or low light environments (Benzing 1990; Théry 2001; Zotz and Hietz 2001)

Often the study of epiphyte distributions takes place over natural gradients of light and humidity within the rainforest habitat. For instance, elevation is often used as a proxy for humidity or rainfall levels, while height in the tree is often used to determine the light and humidity preference of species (eg. Hietz and Hietz-Seifert 1995; Wolf and Flamenco 2003; Krömer et al. 2007). At times, broad zonation systems are used determine the location of an epiphyte within the host tree (ie. Johansson zones; Johansson 1974; ter Steege and Cornelissen 1989; Sanger and Kirkpatrick 2015). While this is acceptable for describing broad patterns in epiphyte distributions, some finer scale partitioning of species along environmental gradients may have been missed. Microclimatic variation within the host tree is not continuous, but often a 'patchy mosaic' within the host tree (Benzing 1995). For instance, differences in the structure and size of branches can lead to differential shading affects, causing variation in light and humidity over small distances (ter Steege and Cornelissen 1989; Cardelús and Chazdon 2005).

Phylogenetic groups appear to respond differently to light and humidity levels as their distributions often vary over the height of the host tree and elevation, which represent strong gradients of these factors. For instance, orchids are often common in more exposed habitats of the outer canopy and lower elevations where the forests are generally drier (Hietz and Hietz-Seifert 1995; Wolf and Flamenco 2003; Krömer et al. 2005, 2007). Ferns also tend to be more common in wetter habitats of sub-montane to montane environments (Wolf and Flamenco 2003; Krömer et al. 2005; Cardelús et al. 2006).

No comprehensive ecological studies have been undertaken on vascular epiphytes in the Wet Tropics region of Australia, despite the area having the highest diversity of epiphytes in the country. Indeed, very few studies have examined the ecology of Australia's vascular epiphytes (Wallace 1981; Cummings et al. 2006; Freiberg and Turton 2007; Sanger and Kirkpatrick 2015). There has been no work on Australian vascular epiphytes that reports the relationships between the distribution of species and environmental variables, using environmental data collected for individual plants. The present study uses such data for light and humidity to examine the environmental relationships of taxonomic groups of vascular epiphytes, and the species within each group. Specifically, we ask: 1) What are the patterns of light and humidity in the epiphytic environment?; 2) How do the

distributions of these groups vary over gradients of light and humidity?; and 3) How do the species within the groups vary over gradients of light and humidity?

3.3 Methods

3.3.1 Study Site

The study was located in the World Heritage listed Mt Lewis region of north-east Queensland, Australia (16°30' S, 145°12' E). The area has tropical rainforests which contain many endemic, Gondwanan-derived plant species (Ramsay and Cairns 2004). The study site was located in Brooklyn Wildlife Sanctuary, a conservation area and nature reserve managed by the Australian Wildlife Conservancy and the adjacent Mt Lewis National Park. The lower elevations of the study site contain complex notophyll vine forest, while above 900-1000 m asl is simple microphyll vine-fern forest (Tracey 1982). The mean average annual temperature near the summit of Mt Lewis (1210 m asl) is 19°C, with average annual rainfall exceeding 3000 mm (Adam 1994; McJannet et al. 2007). There is a distinct dry season over the winter months (June to November), however, the site is frequently immersed in cloud throughout the year providing an important water source during the drier months (McJannet et al. 2007). The area has been subject to mining activity and partly logged in the past.

On each tree, each individual epiphyte that could be safely reached by climbing methods was surveyed. We estimate that we were able to reach approximately 85-90% of all epiphytes within the tree, the remainder were on outer, unstable branches which could not be safely reached. We included holo-epiphytes, hemi-epiphytes and nomadic vines. Holo-epiphytes are epiphytes which have no connection to the ground for their entire lifecycle (Kelly 1985; Benzing 1990). Hemi-epiphytes begin their lifecycle as true epiphytes but as they grow send roots down the trunk of the host and establish a connection to the ground (Kress 1986; Benzing 1990). Nomadic vines are climbing plants. While ecologically different to holo-epiphytes they do at times lose their connection to the ground (Wallace 1981; Moffett 2000; Zotz 2013b).

For each individual epiphyte, species, taxonomic group (orchid, fern or other angiosperms), height from the ground (m) and light (%) were recorded. Species which were not able to be identified in the field were collected and taken to the Australian Tropical Herbarium for identification. Nomenclature follows the currently accepted species names in Australia as defined by the Australian Plant Census (Council of Heads of Australasian Herbaria 2015) and the Australian Orchid Name Index (Clements and Jones 2008). Light estimations were taken using hemispherical canopy photography. This method calculates the total transmitted light for a particular point (Frazer et al. 1999). A Cannon 5D

mark III digital camera (Ohta-ku, Tokyo, Japan) with a Rokinon 8mm f/3.5 HD Fisheye Lens (Gangnamgu, Seoul, Korea) was used to take hemispherical photos approximately 30 cm above each individual epiphyte. To remove the effect of direct solar irradiance, it is recommended to take photos on uniformly overcast conditions, however this was unachievable due to our limited time in the field. To control for direct solar irradiance, all photos were taken in manual mode with adjusted shutter speed and aperture to best suit light conditions. To standardize the photos and to reduce highlights from around the edge of leaves, light levels were balanced using a standardised histogram reference and clarity using Photoshop (Adobe, San Jose, CA, USA) and edge sharpness was applied for each photo. Photos were then analysed using Gap Light Analyser (Frazer et al. 1999) which calculates the percentage of total transmitted light for each image over an entire year by transforming the image pixel positions into angular coordinates (Frazer et al. 1999).

Table 3.1: A list of the host trees surveyed for epiphytes at Mt Lewis. The table shows the tree species name, family, bark type and the number of each species sampled over the five elevations (800 m, 900 m, 1000 m, 1090 m, 1180 m).

Species	Family	Bark	800m	900m	1000m	1090m	1180m
Argyrodendron sp. Mt Haig F.Muell.	Malvaceae	fissured				5	5
Athertonia diversifolia C.T.White	Proteaceae	coarse					1
Beilschmiedia collina B.Hyland	Lauraceae	coarse					1
Buckinghamia celsissima F.Muell. Mueller	Proteaceae	coarse		1			
Caldcluvia australiensis (Schltr.) Hoogland	Cunoniaceae	coarse			1		
Cardwellia sublimis F.Muell. Mueller	Proteaceae	coarse		3			
Ceratopetalum succirubrum C.T.White	Cunoniaceae	fissured		3	1		
Cryptocarya angulate C.T.White	Lauraceae	coarse			1		
Doryphora aromatica (F.M.Bailey) L.S.Sm.	Atherospermataceae	coarse				1	
Elaeocarpus sericopetalus F.Muell.	Elaeocarpaceae	coarse	1				1
Elaeocarpus sp. F.Muell.	Elaeocarpaceae	coarse	1				
Endiandra jonesii B.Hyland	Lauraceae	coarse				1	
Endiandra leptodendron B.Hyland	Lauraceae	coarse				1	
Endiandra sp. Mt Bellenden Ker B.Hyland	Lauraceae	coarse	1				
Franciscodendron laurifolium (F.Muell.) B.Hyland & Steenis	Malvaceae	coarse			1		
Gillbeea whypallana Rozefelds & Pellow	Cunoniaceae	coarse		1			
Garcinia zichii W.E.Cooper	Clusiaceae	coarse	1				
Pouteria euphlebia Aubl.	Sapotaceae	fissured	3	1			
Pouteria pearsoniorum Aubl.	Sapotaceae	coarse	1	1			
Pouteria sp. Aubl.	Sapotaceae	fissured			1		
Sloanea australis (Benth.) F.Muell.	Elaeocarpaceae	fissured			3		
Sloanea macbrydei F.Muell.	Elaeocarpaceae	coarse			2	2	1
Symplocos sp. Jacq.	Symplocaceae	fissured	2				
Synima cordierorum (F.Muell.) Radlk.	Sapindaceae	coarse					1

Two temperature and relative humidity loggers were placed at each of the five sites (n = 10), one in the inner canopy and one at the base of the tree, one metre from the ground. Each data logger was placed on the southern side of the tree in a position that ensured that it would not be within direct sunlight for any part of the day. Data loggers were left in the field from the 12th of July to the 30st of August 2014, which represent the dry season (driest months are August and September). Temperature and humidity recordings were made every 25 minutes continuously during this time. The average of maximum daily vapour pressure deficit (VPD, KPa) was calculated from the temperature and humidity data for each data logger. Individual epiphytes growing above the mid-way point of the trunk were assigned the VPD from the canopy data logger at that particular site. Similarly, epiphytes growing below the mid-point were assigned the VPD value from the data logger at the base of the tree for that particular site.

3.3.3 Data Analysis

The differences in VPD over the five elevation sites (800 m, 900 m, 1000 m 1000 m, 1090 m and 1180 m) and position within tree (base vs. canopy) were tested with a two-way Analysis of Variance (ANOVA). Epiphyte species were divided into one of three taxonomic groups: Ferns (belonging to the class Polypodiopsida and also includes fern allies belonging to the family Psilotaceae), orchids (Orchidaceae) and other angiosperms (angiosperms other than orchids, including the families: Araliaceae; Araceae; Ericaceae, Moraceae; Pandanaceae; Piperaceae). Only species which had frequencies over ten and individuals recorded on at least three trees were included in the analyses (n = 1624). One way ANOVA's were used to test for differences in light and VPD between the taxonomic classes and the species within the classes. There was no effect of bark type (PERMANOVA; Pseudo-F: 1.388; P = 0.173) on epiphyte species composition, therefore bark type was not included in any of the models. The ANOVA tests were completed in Minitab 16.1.0 (MINITAB, Pennsylvania, USA) and the PERMANOVA was completed in Primer v.6 with PERMANOVA+ add-on software (Primer-E Ltd, Plymouth, UK).

3.4 Results

A total of 42 species were recorded, however only 30 species had abundances greater than ten and were found on three or more host trees. There were 12 fern, 10 orchid and 8 other angiosperm species. The complete list of species can be found in Appendix 3. There were differences in VPD by site and the position in host tree, with an interaction (ANOVA; F-value: 12.26; P < 0.001; Fig 3.1). VPD was higher in the canopy at the 800 m site, followed by the 900 m and then the 1000 m, 1090 m and 1180 m sites. VPD at the base of the host trees was the lowest and there was little difference between the sites.

There were differences in the average light (ANOVA; F-value: 198.25; P < 0.001) and average VPD between the three taxonomic groups (ANOVA; F-value: 207.04; P < 0.001; Fig. 3.3). Orchids had the highest light levels and VPD (27% and 0.43 KPa, respectively), followed by the ferns (21% and 0.28 KPa) and then the other angiosperms (17% and 0.2 KPa).

There were differences in light between the species of the fern (ANOVA; F-value: 46.97; P < 0.001), orchid (ANOVA; F-value: 18.46; P < 0.001) and other angiosperms groups (ANOVA; F-value: 15.46; P < 0.001; Fig. 3.4). There was also a difference in VPD between the species in the fern (ANOVA; F-value: 48.23; P < 0.001), orchid (ANOVA; F-value: 18.01; P < 0.001) and other angiosperms groups (ANOVA; F-value: 5.41; P < 0.001; Fig. 3.4).

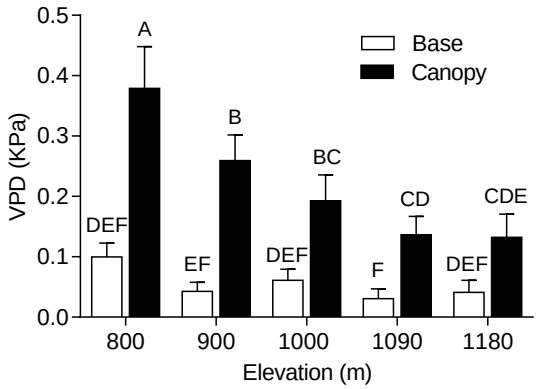

Figure 3.1: Differences in the mean maximum daily VPD over the five elevation sites and between the canopy and base of the host trees. Different letters denote significant differences. Error bars show standard error. VPD data was measured during the dry season months of July and August 2014.

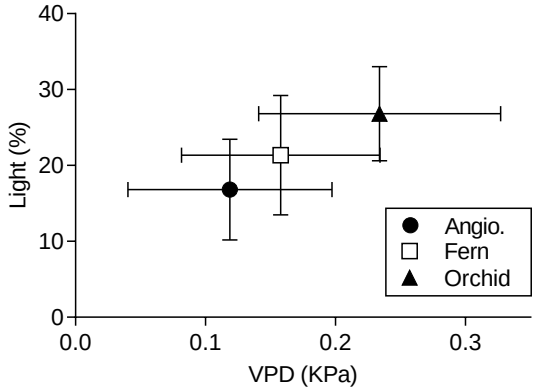

Figure 3.2: The distribution of the three taxonomic groups (ferns, orchids and other angiosperms) over the two environmental gradients, light and VPD. Error bars show standard deviation. VPD data was measured during the dry season months of July and August 2014.

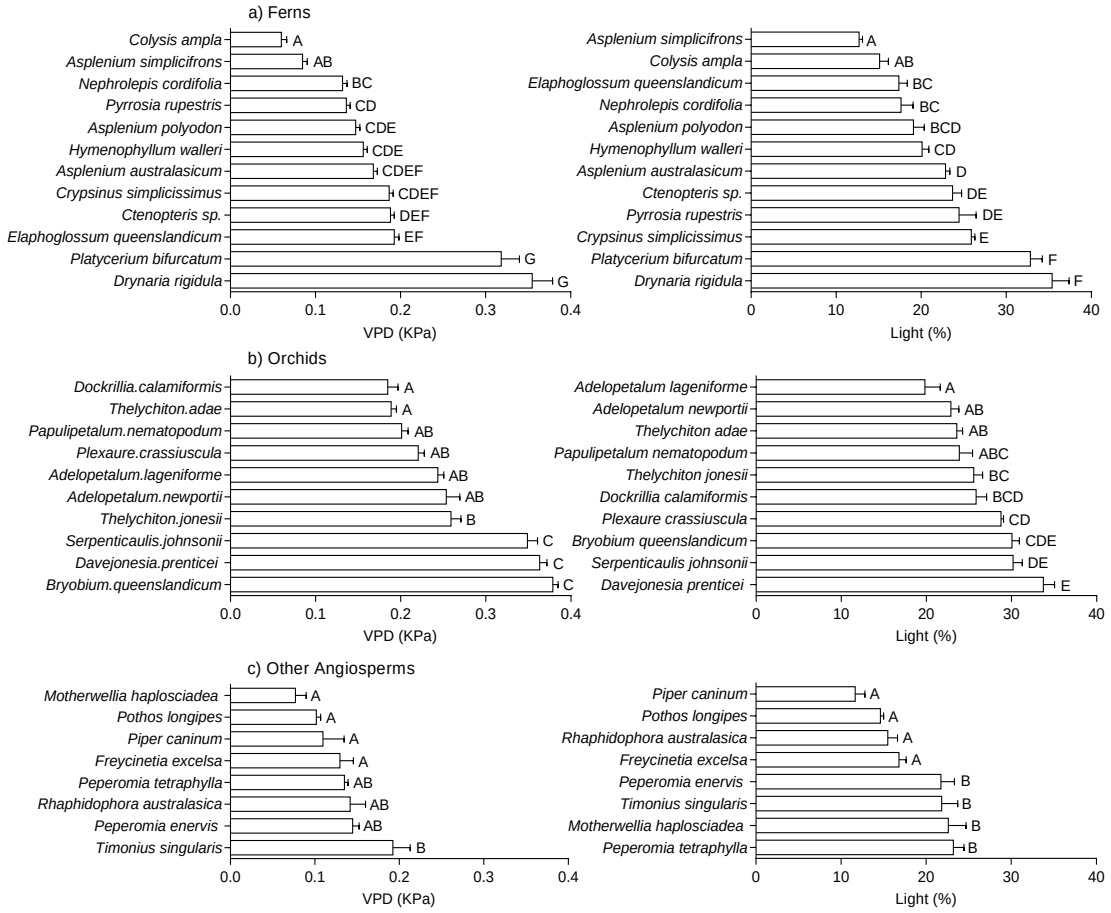

Figure 3.3: The average VPD and light for selected species within the three taxonomic groups: a) ferns, b) orchids and c) other angiosperms. Only species with abundances greater than ten are shown in this graph. Different letters signify differences at $P < 0.05$. VPD data was measured during the dry season months of July and August 2014.

3.5 Discussion

Epiphytes showed distinct partitioning across the host tree and elevation, which represent strong gradients of light and moisture (Wallace 1981; Théry 2001; Wolf and Flamenco 2003; Cardelús et al. 2006; Romanski et al. 2011; Ding et al. 2016). By directly measuring light and VPD, we were able to directly show the strong partitioning of the taxonomic groups over the light and humidity gradients. Furthermore, our results highlight the niche separation of species within each taxonomic group.

The orchids occupied the driest and sunniest ends of the gradients, which is consistent with the literature. Orchids are often found in the most exposed outer branches of the host tree (Krömer et al. 2007) which are low humidity, high light environments. Furthermore, orchids are more dominant in the lower elevations, where conditions are generally drier (Wolf and Flamenco 2003; Krömer et al.

2005; Sanger and Kirkpatrick 2015), although some exceptions do exist (Hietz and Hietz-Seifert 1995; Cardelús et al. 2006; Ding et al 2016). Orchids tend to have the most conspicuous morphologies to cope with drought, such as pseudobulbs, thickened leaves and specialised roots (Benzing 2004; Higgins 2004). Additionally, two-thirds of Australia's orchid species have Crassulacean Acid Metabolism (CAM) photosynthetic pathways (Winter et al. 1983), an adaption which helps reduce water loss through nocturnal uptake of CO_2 (Winter 1985).

The position of the ferns in the middle of both the light and VPD gradients reflected the morphology and physiology of these species. Ferns do exhibit some traits to cope with drought, such as thickened leaves and morphologies such as baskets which accumulate litter that assist in retaining moisture around the roots (Wallace 1981). However, these traits are only present in a few species and CAM is rare in fern species in Australia (Winter et al. 1983). Ferns are most common in the inner canopy of host trees, where light and humidity levels are at intermediate levels (Wallace 1981). Furthermore, ferns are often more dominant in sub-montane and montane forests where humidity levels are higher (Hietz and Hietz-Seifert 1995; Wolf and Flamenco 2003; Krömer et al. 2005; Cardelús et al. 2006).

The distribution of the other angiosperms is best explained by the main growth form in this taxonomic group. Most of the species were nomadic vines, which start their lifecycles attached to the ground. As a result, most of these species were limited to the lower proportions of the host tree, where light levels were at their lowest and humidity is high. This pattern has been found in other Australian rainforests (Sanger and Kirkpatrick 2015).

Despite large differences of light and humidity between the taxonomic groups, there was significant variation between species within the groups. This shows distinct partitioning of taxonomically related species along environmental gradients. Many of the species growing at the most xeric and exposed ends of the gradients had ecomorphological traits that suited the extreme environments in which they grow. For instance, the two fern species occupying the driest environments, *Platycerium bifurcatum* and *Drynaria rigidula*, are both basket ferns which accumulate litter that assist in retaining moisture around the roots (Wallace 1981).

There was a tendency for epiphytes that grew in well-lit positions to also grow in positions with high VPD. This is expected as the most exposed, high light environments are in the canopy of the host trees, where, due to higher temperatures, VPD is also higher. However, some exceptions do exist. For instance, *Dockrillia calamiformis* and *Pyrrosia rupestris* occurred in low VPD and high light environments, which was a reflection of their preference for outer canopy habitats at higher

elevations. *Motherwellia haplosciadea* also occurred in low VPD and high light environments. As a nomadic vine, it may have found patches of light within the more humid lower sections of the host tree. *Elaphoglossum queenslandicum,* showed the opposite pattern, with high VPD and low levels of light, which suggests it is more common in the lower elevations at shadier locations.

The Wet Tropics Region has a distinct dry season, which can lead to high rates of mortality among epiphytes in the lowland areas (Freiberg and Turton 2007). However, as our study site was located at a higher elevation, the impacts of the dry season may be less severe. This is due to occasional moisture inputs from low level cloud and fog, which can still occur during the dry season.

While our study shows a response of epiphyte species to light and VPD, these factors alone only partially explain the composition of vascular epiphytes (Benzing 1990; Ding et al. 2016). Light only explained 22% of variation in epiphyte composition in the subtropical rainforests of Australia (Sanger and Kirkpatrick 2015). Furthermore, environmental factors in the lowland forests of Panama explained as little as 10% (Zotz and Schultz 2008).

There are many other aspects apart from light and VPD which determine the distribution of epiphytes within the physical environment. Some studies suggest that dispersal limitations may have more of an influence on epiphyte distributions than microclimate (Wolf 1994; Krömer et al. 2007; Ruiz-Cordova et al. 2014). Our observations do not allow us to reject vagility as a cause of species patterning at the site scale, although the distances are not great, and most species have dust seeds or spores. The structure and branching patterns of the host tree can influence light and air movement which can affect epiphyte composition (ter Steege and Cornelissen 1989; Cardelús and Chazdon 2005). Furthermore, humus and thick layers of bryophytes can accumulate on large branches, which can provide habitat for an assemblage of different vascular epiphyte species (Nadkarni 1984; Ingram and Nadkarni 1993; Woods et al. 2015).

Our study suggests that vascular epiphytes show distinct partitioning over gradients of light and VPD. This partitioning is evident both within and between taxonomic groups. This suggests that microclimatic factors play an important role in determining the realised niche of epiphytes within the tropical Australian rainforests.

Chapter 4

The distribution of the morphological and physiological traits of epiphytes within trees and between elevations in subtropical Australian rainforest

4.1 Abstract

Epiphyte species have been shown to have similar morphological and physiological traits to each other in similar environmental conditions, however, many studies that record this phenomenon are either restricted to a single taxonomic group or cover small spatial scales. We ask whether rainforest epiphyte species that occupy comparable realised niche spaces along a moisture gradient have similarities in taxonomy, morphology or physiology. Vascular and moss epiphytes were surveyed within four height zones at five elevations (300-1100 m asl) in the sub-tropical rainforest of Australia. Epiphyte species distributions were agglomeratively classified using Ward's method. Chi square was used to test for differences in the incidences of taxonomic groups, lifeforms, leaf thickness, photosynthetic pathways and other drought-mitigating morphologies in the groups. Six species groups were identified. Vascular epiphytes with CAM, thickened leaves and other drought-mitigating morphologies were common in the groups that occupied the most xeric situations. Vascular species with little to no drought-mitigating characteristics were common in groups that occupied moister situations. Moss morphologies were less congruent with environmental conditions than vascular plant morphologies. Vascular epiphyte species tended to have morphological and physiological traits which appeared suitable for their environment, while some moss species had morphologies that seemed inappropriate for the environments they occupied.

4.2 Introduction

Epiphytes use other plants for mechanical support and have no direct connection to the ground, relying on moisture and nutrient inputs from fog and rainfall (Benzing 1990). They therefore tend to be more limited by moisture availability than most terrestrial plants (Zotz and Hietz 2001). Lack of water is postulated to be the greatest stress on vascular and bryophytic epiphytes (Zotz and Hietz 2001; Sillett and Antoine 2004; Romanski et al 2011; Bartels and Chen 2012).

Many vascular epiphytes exhibit physiological and morphological characteristics which help them cope with drought. Some have Crassulacean Acid Metabolism (CAM) photosynthetic pathways, which help reduce water loss through nocturnal uptake of CO_2 (Winter 1985). Many vascular epiphytes have specialised morphologies that assist with water retention, such as thickened or

succulent leaves, or rhizomes and specialised water storage tissue (Hietz and Briones 1998; Benzing 2004; Higgins 2004; Reyes-García et al. 2008; Zhang et al. 2015).

Epiphytic bryophytes have adapted to drought in different ways to vascular epiphytes. All bryophytes, except one order of hornworts (Anthocerotales), use the C_3 pathway for photosynthesis, a process which is less water efficient than CAM (Smith and Winter 1996; Raven et al. 1998; Hanson and Rice 2013). Instead, bryophytes, and some pteridophyte species, are poikilohydric, in that they can rehydrate upon wetting from a desiccated state (Proctor 1990; Bates 1998; Sillett and Antoine 2004). Bryophytes also have a range of forms, which can assist in water storage (ver Leerdam et al. 1990; Hedenäs 2001; Frahm 2003; Sillett and Antoine 2004). For example, bryophytes that form dense mats can store water in the capillary spaces between the leaves (Bates 1998; Frahm 2003; Sporn et al. 2010).

Within the host tree, light, temperature, wind, atmospheric composition and moisture vary from the moist, shaded base of the trunk to the more arid and exposed outer branches (Wallace 1981; Théry 2001; Bartels and Chen 2012). Distinct patterns in the distributions of morphological and physiological traits of epiphytes occur within the host tree (Pittendrigh 1948; Johansson 1974; Hietz and Briones 1998; Reyes-Garcia et al. 2012). Vascular epiphytes inhabiting the shadier and more humid lower zones of the tree tend to have fewer traits associated with drought-resistance, while species with traits such as CAM, succulence, thickened and smaller leaves are common in the sun-exposed outer crown (Johansson 1974; Winter et al. 1983; Hietz and Briones 1998). Bryophytes lifeforms which assist in the storage of water, such as mats, occur in the exposed parts of the canopy, while light-gathering bryophytes, such as dendroids, are more common in the shady bases of host trees (Bates 1998; Acebey et al. 2003; Silva and Porto 2013).

At the landscape scale, moisture and temperature vary with elevation, with montane environments frequently shrouded in cloud, resulting in high levels of absolute humidity and rainfall (Chantanaorrapint 2010; Strong et al. 2011; Ding et al 2016). There are distinct distributions of morphological traits in both epiphytic and terrestrial ferns with elevation in Hawaii, with more divided fronds at higher elevation, longer blades in shaded habitats, and fronds with shorter stipes and fewer pinnae in drier habitats (Creese et al. 2011). Macro-lichens have a high level of branchiness at higher elevations, which is inferred to be a response to high levels of fog (Stanton and Horn 2013).

Many studies which describe the distributions of epiphyte morphologies and physiologies are restricted to within the host tree. There are few that cover landscape gradients (e.g. Mantovani

1999) and none that cover both gradients. In the present study we assess which vascular and moss epiphytes share similar niche spaces within the host tree and across elevational zones. We determine whether species with similar distributions have comparable morphological and physiological characteristics. For instance, we expect that species that are common at the more xeric ends of the gradients will have morphologies and physiologies that assist with water retention. Conversely, shade-tolerant life forms or species with fewer traits associated with drought-resistance should be more common at the opposite end of the gradient.

4.3 Methods

4.3.1 Study Area

The study was conducted in the Border Ranges National Park (28°21'35"S, 152°59'10"E), a world heritage listed subtropical rainforest that covers 3,600 km2 in northern New South Wales, Australia. A set of long term monitoring plots, along a transect ranging from 300 to 1100 m in elevation, with plots at 200 m intervals, is located on the western side of the Border Ranges National Park (Kitching et al. 2011). Further details of the study site and general patterns of epiphyte distribution on this transect can be found in Sanger and Kirkpatrick (2015).

While there are no detailed climate data available for the long term monitoring plots at the Border Ranges, detailed climate information exists for a transect of similar design at Lamington National Park, which is located 20 km from the Border Ranges transect in the same mountain range (Strong et al. 2011). The average annual temperature decreased by 0.75 ^{o}C with every 100 m gain in elevation, equating to a difference of 6-7 ^{o}C between 300 and 1100 m (Strong et al. 2011). During the drier months (August and September), relative humidity at midday increased linearly from the 300 m site (canopy: 25%; understorey: 45%) to the 1100 m site (canopy: 60%; understorey: 80%; Strong et al. 2011). There was little difference in humidity during the wet season (February and March), with humidity levels at close to 100 percent within the canopy and understory at most elevations (Strong et al. 2011).

4.3.2 Epiphyte sampling

We collected our data from trees in the elevation plots at Border Ranges between May and July 2013. Within each of the five elevations along the transect, ten suitable large trees closest to the centre of the plot were selected. Trees were selected for their suitability for climbing (healthy trees with no obvious signs of rot, with large sturdy branches within 30 m of the ground, unobstructed by large woody vines). Trees were climbed using a combination of single and double rope techniques (Lowman and Moffett 1993). The species, height, tree diameter at breast height (DBH), measured at

a height of 1.3 m, and the elevation and GPS location were recorded for each host tree. Fifteen tree species from ten families were sampled (see Table 2.1).

Each tree was divided into height zones, adapted from the zonation system used by Johansson (1974). Following ter Steege and Cornelissen (1989), Romanski et al. (2011) and Gehrig-Downie et al. (2011), we divided the trunk into two zones, as the upper trunk often had a very different microclimate to the lower trunk. Four height zones were surveyed: inner canopy (the inner third of the branches in the crown), the upper trunk (the mid-point of the trunk to the first bifurcation) the lower trunk (two metres above the base of the trunk to the mid-point of the trunk) and the base (from the ground to 2 m). The outer and mid canopy were not surveyed as these zones are often difficult to access safely. In each height zone of each tree, the number of individuals of each species of vascular epiphytes was recorded. Clumped or rhizomatous plants were counted as one individual, following Sanford (1967). Specimens that could not be identified in the field were collected and taken to the Queensland Herbarium (BRI) for identification.

We wished to produce a list of moss taxa for each zone on each tree. Due to the patchiness of bryophytes within the host trees, randomly place quadrats (Gradstein et al. 1996) were not used, as richness would have been underestimated. Following Wolf (1993), subsamples were collected from different microenvironments within the zone or wherever there appeared to be a distinct change in bryophyte species composition. Ten to 15 subsamples were normally collected from each zone. Samples were taken to the Queensland Herbarium for sorting into morphospecies and identified to either genus or species level where possible. No cover estimates or abundance data were recorded. We focused on mosses to reduce the likelihood of missing rare or inconspicuous cryptogam species. Nomenclature for both vascular and non-vascular species follows the Catalogue of Life (Roskov et al. 2015). Herbarium vouchers were deposited in the Queensland Herbarium, Brisbane.

The life form of each epiphyte was noted. Vascular epiphytes were placed into one of three categories: holo-epiphytes, hemi-epiphytes and nomadic vines. Holo-epiphytes spend their entire life cycle on the host tree without connection to the ground or the vascular system of the host (Kelly 1985; Benzing 1990). Hemi-epiphytes are plants that begin their life cycle as true epiphytes but later send feeder roots down the trunk of the host tree and connect to the ground (Kress 1986; Benzing 1990). Nomadic vines, such as species belonging to the genera *Phymatosorus*, *Arthropteris* and *Pothos*, are climbers. While they are ecologically different to epiphytes, they do have adventitious roots are often used for nutrient and water uptake and they occasionally lose their connection to the ground (Wallace 1981; Moffett 2000; Zotz 2013b). Five types of moss life form were identified:

dendroid, pendant, mat, tuft and weft, based on Bates (1998), Kürschner et al. (1999) and Frahm (2003).

For each epiphyte species, features such as thickened, glossy, leathery or reduced leaves, pseudobulbs, and the presence of detritus-collecting baskets were also recorded for each species as 'other drought morphologies', as determined from field observations and from Wilson (1990) and Bernhardt (1993). The presence of CAM in vascular species or the presence of poikilohydry in mosses and some fern species was noted. For the vascular species, the presence of CAM or C_3 pathways followed Winter et al. (1983), who assessed the CAM status of 157 vascular epiphytes from Australia by examining the stable carbon isotope ratio ($\delta^{13}C$) values and the absence of Kranz anatomy. Species are classified as CAM plants if $\delta^{13}C$ values were less than -20 ‰. Twelve species found in the current study were not assessed by Winter et al. (1983), with most of these species being nomadic vines. All moss species are known to use the C_3 pathway (Smith and Winter 1996; Raven et al. 1998; Hanson and Rice 2013).

4.3.3 Data analysis

The presence/absence of each vascular and moss species was noted for each height zone for each tree surveyed. The data were then summed across the ten tree replicates at each site to create a frequency of species occurrence within each of four height zones over each of the five elevations (n = 20). Ward's technique for agglomerative cluster analysis (Ward 1963) was used on a Euclidean distance matrix to identify groups of species with similar distributions in the 20 elevation by tree zone samples. Non-metric multidimensional scaling (MDS) plots were created to visually depict differences in the species groups derived from the cluster analysis over the height zone and elevation gradients.

Chi square was used to test whether the proportions of species in the distributional groups differed at $p < 0.05$ in taxonomic group (orchids, ferns and mosses), photosynthetic pathway (CAM or C_3), lifeform (nomadic vine, holo-epiphyte, dendroid, pendant, mat, tuft and weft) or other drought morphologies (presence of pseudobulbs, thickened or leathery leaves etc.). The expected values were calculated from the proportions of the types within the species list as a whole. Classification and chi square tests were performed using Minitab 16.1.0 (MINITAB, Pennsylvania, USA). MDS plots were created using Primer v.6 with PERMANOVA+ add-on software (Primer-E Ltd, Plymouth, UK).

4.4 Results

Thirty-four species of vascular epiphytes (17 species of fern, 13 species of orchid and four species of dicotyledonous plants) and 42 morphospecies of moss were recorded. The lifeform, photosynthetic

pathway and other drought morphologies for each species is listed in Appendix 4. The cluster analysis showed six distinct groups (Fig. 4.1). Each group contained species which had similar distributions over the height and elevation gradient (Fig. 4.2). Group 1 consisted of species that inhabited the lower tree height zones and had a broad distribution over the elevation gradient. The species in Group 2 occurred in the more xeric ends of the two gradients: the upper height zones and lower elevations. Group 3 consisted of species that had distributions over the mid to upper height zones and were distributed mainly around the mid elevations. Group 4 had species which occurred in the upper height zones and the high elevations. Group 5 contained species that were present in the higher elevations and occurred over the entire tree height gradient and Group 6 contained species that occurred in the upper height zones across all elevations. The three dimensional MDS plot had a lower stress value (3D Stress: 0.14) than the two dimensional MDS plot (2D Stress: 0.22). Each group occupied a largely distinct space in at least one of the axis configurations (Fig. 4.3). Groups 1 and 5 were less differentiated on the graphs than other pairs of groups, as were Groups 2 and 6. In the spaces defined by axes 1 and 2, and 2 and 3, the distinct extreme groups were 1 and 2.

Group 6 had more fern species (Chi^2: 7.06; df = 1; p = 0.008) and fewer bryophytes (Chi^2: 4.40; df = 1; p = 0.034) than would be expected by chance. Group 2 had a significantly higher proportion of orchids (Chi^2: 7.86; df = 1; p = 0.005). Groups 1, 2 and 4 had an even mix of mosses and vascular species, while Groups 3 and 5 were dominated by mosses. The five species of nomadic vine all belonged to Group 1 (Chi^2: 10.16; df = 1; p = 0.001). Six of the nine species in group 5 were tuft mosses (Chi^2: 11.39; df = 1; p < 0.001). There were a higher proportion of holo-epiphytes in groups 6 than expected by chance (Chi^2: 11.39; df = 1; p < 0.001).

Group 2 had a significantly higher proportion of known CAM species (Chi^2: 5.45; df = 1; p = 0.02). All other groups either had no species exhibiting CAM (Groups 1 and 5) or contained only one or two CAM species (Groups 3, 4 and 6). Species in Group 2 (Chi^2: 9.24; df = 1; p = 0.002) and Group 6 (Chi^2: 4.31; df = 1; p = 0.04) had a higher proportion of species with other drought-mitigating morphologies, while Group 1 (Chi^2: 5.58; df = 1; p = 0.02) and Group 5 (Chi^2: 5.38; df = 1; p = 0.02) contained no species with other drought-mitigating morphologies.

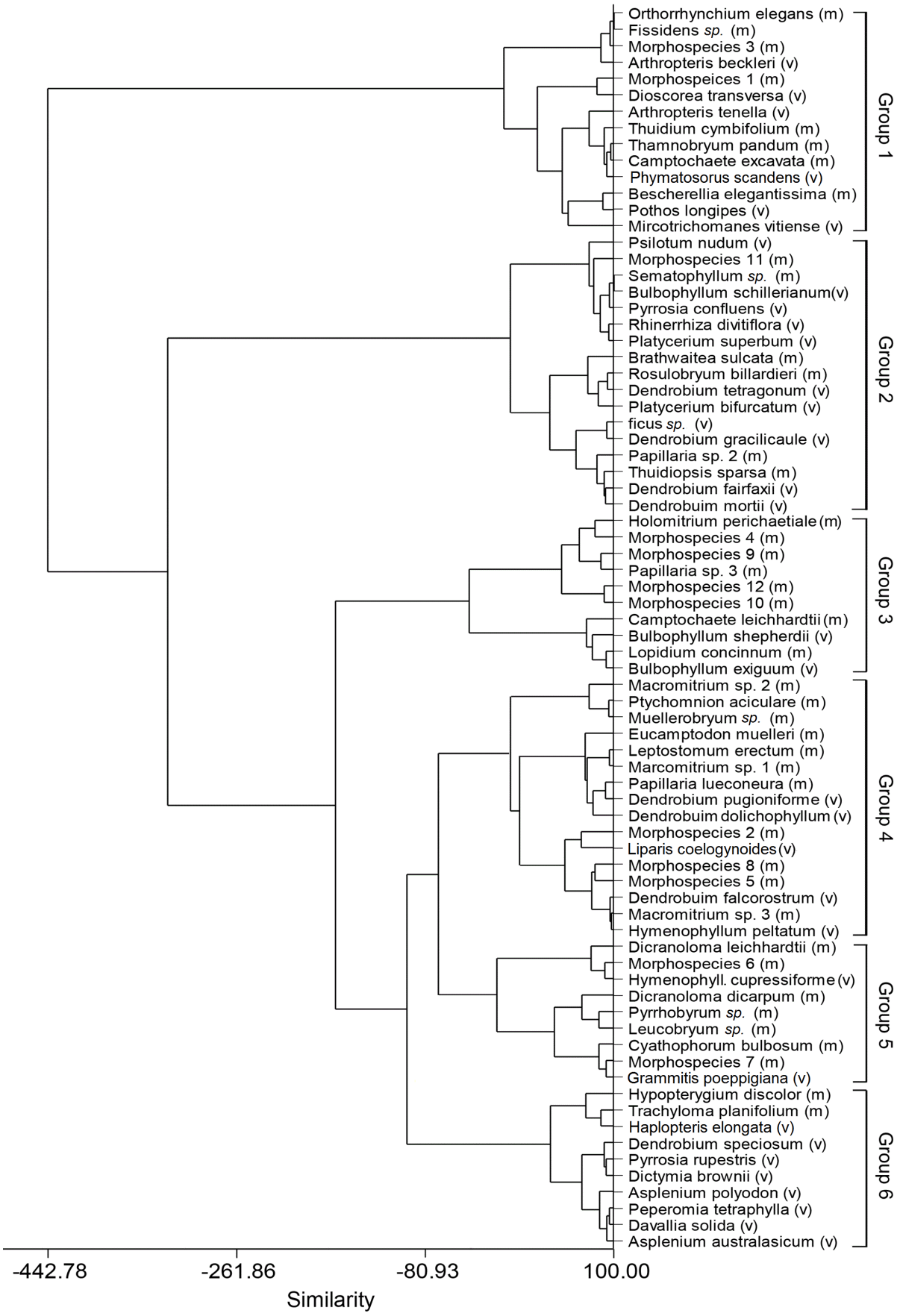

Fig. 4.1: Dendrogram showing the six groups of vascular (v) and moss (m) species with similar distributions over the two gradients: tree height and elevation.

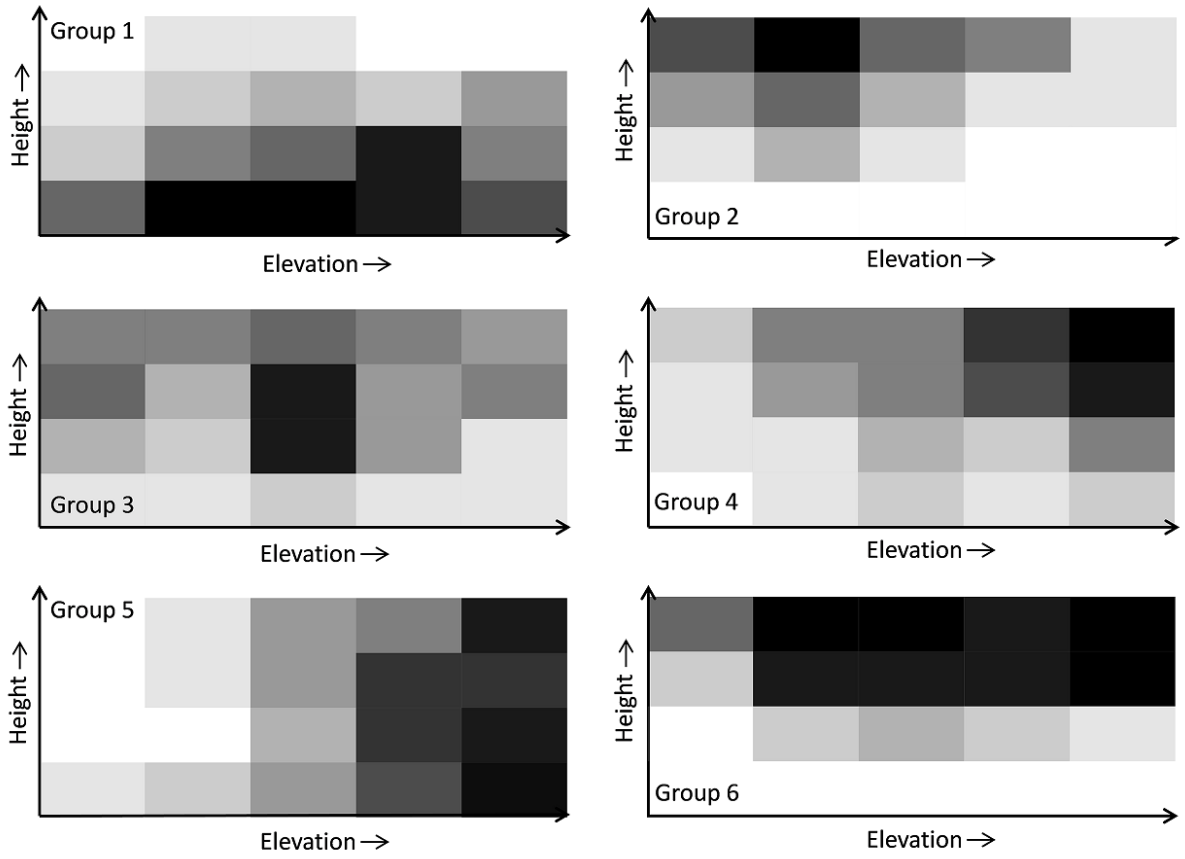

Fig. 4.2: The epiphyte species richness over the height and elevation gradients for each group. Shading represents the number of species in each height zone / elevation, with the lightest shade of grey representing one species and black representing all species in the group.

4.5 Discussion

The vascular species occurring in the most xeric ends of the height zone and elevation gradients (Group 2) tended to have ecomorphological and physiological characteristics that would allow them to endure drought. Along with a high proportion of orchids in this group, there was a high number of species with CAM, an adaptation possessed by approximately two-thirds of Australia's orchid species (Winter et al. 1983; Holtum and Winter 1999). *Pyrrosia confluens*, one of the few Australian fern species to exhibit CAM (Winter et al. 1983) was also in the group. The occupation of the driest and most exposed habitats by CAM epiphyte species is widespread, having been noted in lowland forest in Panama (Zotz and Ziegler 1997), Trinidad (Griffiths and Smith 1983) and in Australia (Winter et al. 1983). CAM has also been found to be more prevalent in vascular epiphytes at low elevations where climatic conditions are drier (Earnshaw et al. 1987; Silvera et al. 2009)

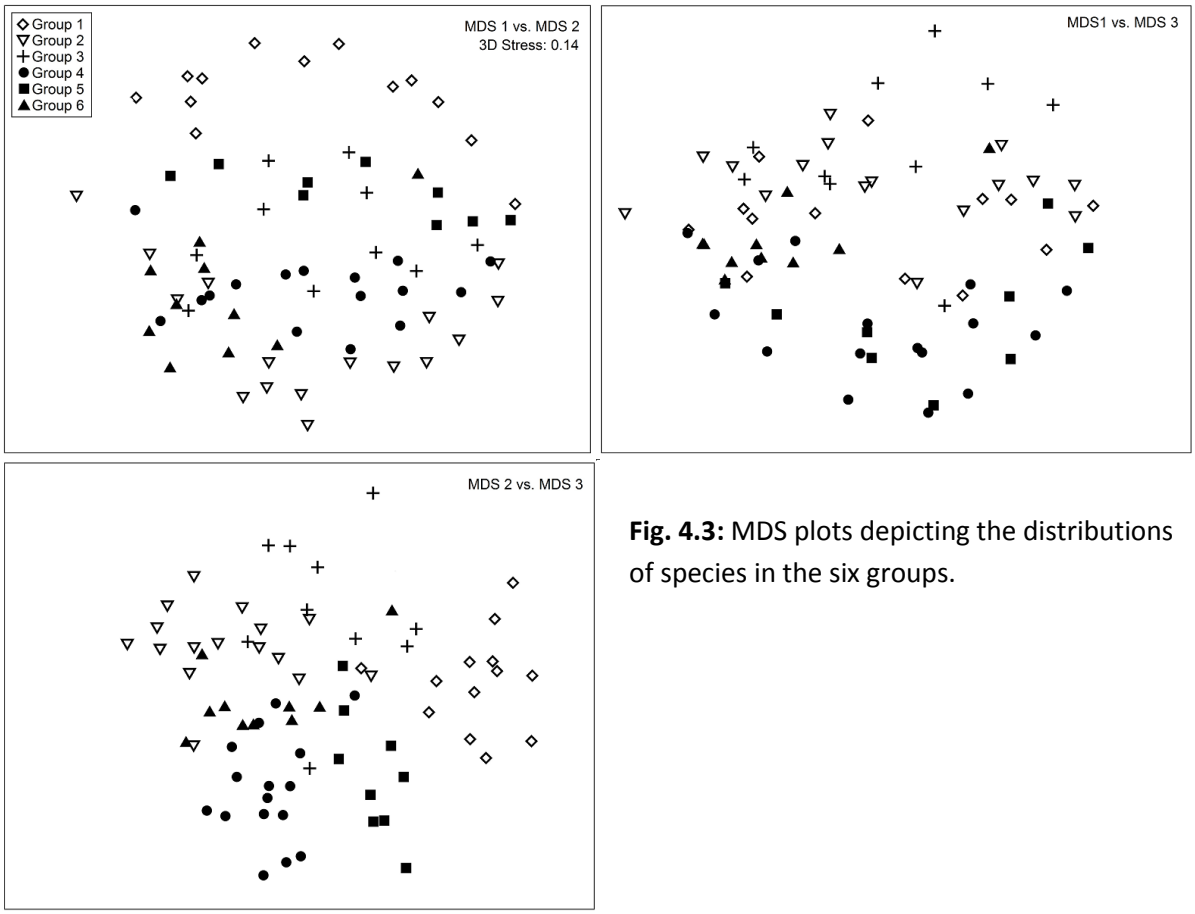

Fig. 4.3: MDS plots depicting the distributions of species in the six groups.

In addition to a high number of species with CAM, Group 2 had a high number of species with thick leaves, a trait that has been found to assist in water retention (Hietz and Briones 1998; Benzing 2004). This occurrence of vascular epiphytes with thick leaves in dry microsites is also widespread (Pittendrigh 1948; Johansson 1974; Hietz and Briones 1998; Mantovani 1999). Group 2 also had a high proportion of species with other drought-mitigating features. For example, *Platycerium bifurcatum* and *P. superbum* are nest-forming ferns which accumulate litter and dead fronds that assist in retaining moisture around the roots (Wallace 1981). *Platycerium bifurcatum* also has specialised water-storage tissue (Kreier and Schneider 2006) and the epidermis of its sporotrophophyll leaves are covered by hairs which decrease water loss (Rut et al. 2008). The orchids in Group 2 possessed other morphological characteristics that would help them resist to drought, such as specialised root systems and pseudobulbs (Benzing 2004; Higgins 2004).

The majority of the vascular species that had no morphological characteristics to cope with drought occurred in species groups distributed over the wetter ends of the two gradients, a pattern which

has been observed elsewhere (Johansson 1974; Hietz and Briones 1998). Only plants with C_3 pathway, thin leaves and no other obvious drought-mitigating morphologies occurred in the groups distributed over the low height zones and high elevations (Groups 1 and 5), which may reflect constantly high humidity in these locations. The ordination of species further highlights the distribution of the groups over the moisture gradient, with Group 1 having the greater distance from Group 2 in the MDS plot.

Vascular epiphytes in the groups distributed over habitats which represented intermediate moisture levels had some drought-mitigating features. The species in Group 6, which occurred over the more humid mid to high elevations were subject to some drought stress as they were restricted to the upper height zones and would be exposed to intermittent dry periods between rainfall events. While there was not a significantly higher proportion of CAM in this group, there were a high proportion of other drought-mitigating morphologies. This group was dominated by ferns, which generally occupy wetter habitats than orchids (Wallace 1983; Benzing 2004) and have features such as leathery or glossy leaves or basket formations.

While we found clear distribution patterns in the morphology and physiology of vascular species related to the moistness of the environment, the distribution of moss morphologies were less clearly related. Overall, bryophytes were dominant in groups which were distributed over the mid to high elevations, where there are higher humidity levels and milder temperatures, which is similar to previous observations (Wolf 1994; Benzing 1998; Sillett and Antoine 2004). However, there were many moss species present in the groups which occupied the driest habitats. This may be a reflection of mosses being able to occupy a wide range of niches, from full sun in the driest habitats to shaded moist conditions (Holz et al. 2002; Acebey et al. 2003; Romanski et al. 2011; Silva and Pôrto 2013). However, the distribution of only one of the moss lifeforms was consistent with previous ecomorphological observations. Tufts were more common in the high elevation group (Group 5) where humidity levels are high. Tufts appear to be an adaptation for high moisture environments as the form enhances gas exchange by preventing being wetted along tree trunks (Frahm 2003). The majority of other species had lifeforms that appeared inappropriate for the environments occupied by their group. For example, the group of species from the most xeric sites contained pendants, which are usually found at higher elevations where their narrow feathery stems can facilitate the uptake of atmospheric water (Bates 1998; Kürschner et al. 1999; Romero 1999; Frahm 2003; Parolly and Kürschner 2004). Similarly, mats are very effective at storing water in the capillary spaces created between the individuals, making them characteristic of light-intensive, dry micro-climates (Bates 1998; Acebey et al. 2003; Frahm 2003), yet mats occurred in shady and moist

environments. The dendroid lifeform tends to be intolerant to dry habitats due to inefficiencies in their internal conducting system (Frahm 2003), yet this lifeform was common in the groups occupying the driest habitats.

We hypothesise that this seemingly poor fit between moss morphology and microclimate compared to that of the vascular species may be a reflection of differences in scale between the two taxonomic groups. For example, mosses, being much smaller than the vascular species, may be able to occupy tiny areas of moist habitat amongst dry areas, like the shady undersides of branches or small fissures in the bark, whereas the size of vascular plants might preclude such occupance. Vascular species could also alter the microclimate of patches of the inner canopy by creating shade, which could easily be exploited by smaller organisms, such as mosses. A test of the above hypotheses would require detailed mapping of species distributions and micro-habitats on trees, rather than the zonal approach we have adopted.

We acknowledge that there are some limitations in using physiology and morphology data from other studies. For instance, other methods to test for CAM or testing species under drought conditions may yield different results to that reported by Winter et al. (1983). Two basket fern species present in the group occupying the most xeric habitat, *Platycerium bifurcatum* and *P. superbum*, were not identified as CAM plants when tested under non-drought conditions using carbon isotope ratios (Winter et al. 1983). However, CAM is often more easily detected in drought-stressed individuals (Cushman and Borland 2002; Rut et al. 2008). Subsequent studies measuring CAM in *P. bifurcatum* under drought conditions have found that CAM was present in the cover leaves (Rut et al. 2008). Weak CAM has also been found in closely related *Platycerium veitchii* by testing for nocturnal increases in titratable acidity rather than using carbon isotope ratios (Holtum and Winter 1999). However, finding nocturnal acidification under drought stress does not define an epiphyte as being a CAM plant, and species can switch between CAM and C_3 pathways (Winter 1985).

There are many other factors besides micro-climate that could have influenced the distribution of epiphytes in this study. The bark type, age, size and branching structure of the host tree can affect epiphyte distributions (ter Steege and Cornelissen 1989; Benzing 2004; Sillett and Antoine 2004; Bartels and Chen 2012). These host tree characteristics did vary with and between sites and may have impacted on our results. Biotic interactions may have also influenced the distribution of species in this study. Two fern species, *Davallia solida* and *Asplenium ployodon* almost exclusively grow out of the base of *Asplenium australasicum*, where they can take advantage of moisture retained in the canopy soil and detritus caught in the basket (Wallace 1981). Furthermore, bryophytes can

accumulate in thick mats, creating a deep layer of organic matter which can facilitate the colonisation by vascular epiphytes by acting as water and nutrient reservoirs (van Leerdam et al. 1990; Jarman and Kantvilas 1995).

By using objective classification of species groups, and on a new continent for such studies, we have reinforced the generalisation that vascular epiphyte species have sets of morphological and physiological characteristics that are congruent with within tree and elevational variation in environment. Our finding that, at our scale of inquiry, many moss species had morphological characteristics that appeared inappropriate for the environments occupied by their group has led us to propose two hypotheses for future research.

Chapter 5

Fine partitioning of epiphyte habitat within Johansson zones in tropical Australian rainforest trees

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5.1 Abstract

For over three decades, the Johansson zones have been widely used in epiphyte studies as a way of stratifying the host tree into habitat zones. The usefulness of this system, however, has been questioned. We test the effectiveness of the Johansson zones by grouping epiphyte species by the substrate and microclimatic attributes of their individual occurrences and assessing the fidelity of these groups to the Johansson zones. Habitat characteristics were recorded for every individual epiphyte on 30 trees in the lower montane rain forests of north-eastern Australia. Twenty-four epiphyte species were agglomerated into four groups using Ward's method. Group 4 was highly distinct and included shade-loving species and nomadic vines from the lower zones of the host trees. Group 3 contained species from the most exposed habitats. Group 1 had higher light levels and lower substrate thickness than Group 2, yet both groups had close to identical distributions over the Johansson zones. This suggests that groups of epiphyte species may utilize different micro-sites within the same zone. While the Johansson zones are a useful tool in epiphyte studies, finer partitioning of habitat within the host tree may be missed.

5.2 Introduction

Vascular epiphytes, plants which grow on other plants for mechanical support, often show distinct patterns of distribution within host trees (Johansson 1974; ter Steege and Cornelissen 1989; Krömer et al. 2007; Sanger and Kirkpatrick 2015). The turnover of species across this vertical gradient is one of the most commonly studied aspects of epiphyte ecology. As a result, many vertical stratification systems have been developed to correspond with natural zones within the host tree (Zotz 2007). The most popular system was originally developed for emergent host trees in West African rain forest (Johansson 1974). The Johansson zones stratify the host tree into five zones based on the structural position in the tree (i.e., base, trunk, inner canopy; Fig. 1; Johansson 1974). Because of its wide use, the Johansson system is useful for standardized descriptions of epiphyte communities on large trees within forests (Nieder and Zotz 1998). It is less applicable for understory trees or hosts with unusual structure (e.g., palm trees; Krömer et al. 2007; Zotz 2007; Mendieta-Leiva and Zotz 2015). Despite its

wide use, the effectiveness of this system has been questioned, as epiphyte communities often transgress the zones and can be associated with microhabitats more than zonal patterns (Wallace 1981; Bongers 2001; Krömer et al. 2007; Romanski et al. 2011; Woods et al. 2015).

The host tree has many different microclimates. Light varies dramatically from the outer branches of an emergent host tree to the dark shady base of the trunk (Romanski et al. 2011; Sanger and Kirkpatrick 2015; Woods et al. 2015). Similarly, humidity and temperature also differ within the height of the host tree. The outer branches are often subject to periods of low humidity and extreme temperatures, while the base of the tree has temperature and humidity conditions similar to the forest floor (Freiberg 1997; Romanski et al. 2011; Wagner et al. 2013; Woods et al. 2015). The Johansson system divides the tree into microclimatic zones. However, light, humidity, and temperature are often a continuous gradient across the tree rather than forming discrete units (Wallace 1981).

Zonal variation in the structural attributes of the tree can strongly influence the distribution of epiphytes. Horizontal branches often have more suitable attachment points than the trunk (ter Steege and Cornelissen 1989; Benzing 2004). These branches can develop canopy soils that store moisture and nutrients, thereby influencing epiphyte community composition (Nadkarni 1984, Ingram and Nadkarni 1993, Woods et al. 2015). Thick moss mats that are common on large branches may also facilitate the establishment and survival of vascular epiphytes (van Leerdam et al. 1990; Hietz and Hietz-Seifert 1995; Zotz and Vollrath 2003). The inner canopy alone can consist of a patchwork of different microhabitats, from a fork with a thick layer of canopy soil, to the shady underside of a branch, through to a patch of bark exposed to the sun. This diverse array of microhabitats leads to a high diversity of epiphytes in this zone (Krömer et al. 2007; Sanger and Kirkpatrick 2015; Woods et al. 2015). However, these microhabitats are grouped into one Johansson zone and therefore may fail to account for the fine scale variation in habitat (Wallace 1981).

A logical approach to test the utility of any *a priori* zonation of epiphyte habitat is to assess the spatial correspondence of predefined epiphyte communities or individual species to the zonation system. Zotz (2007) evaluated the utility of the Johansson zones in this way, classifying epiphyte communities *a priori* based on the spatial distributions of epiphyte species. He found partial correspondence of these communities with the Johansson zones. However, many other factors rather than spatial position alone determine the realized niche of epiphytes. Complementing the work of Zotz (2007), which was purely based on the position of epiphytes within the host tree, our study took into account the effects of microclimatic and microhabitat variables. We classified species into 'niche groups' based on microclimate, substrate attributes, and position and assessed how well

these niche groups fit with the Johansson zones. In this way we tested, for the first time, the habitat uniformity of the zones.

5.3 Methods

5.3.1 Study site

Observations were made at Mt Lewis (16° 30° S, 145° 12° E) in northeast Queensland, Australia. The area is a World Heritage listed rain forest and home to many local endemic, Gondwanian-derived angiosperm species (Ramsay and Cairns 2004). The study was located on Brooklyn Wildlife Sanctuary, which is owned and managed by Australian Wildlife Conservancy. Our study site was located in the montane rain forests close to the summit of Mt Lewis. These forests are simple microphyll vine-fern forest (Tracey 1982). The mean average annual temperature is 19°C, with average annual rainfall exceeding 3000 mm (Adam 1994; McJannet et al. 2007). The region has a distinct dry season in the winter (June to November); however, the site is frequently immersed in cloud throughout the year (McJannet et al. 2007).

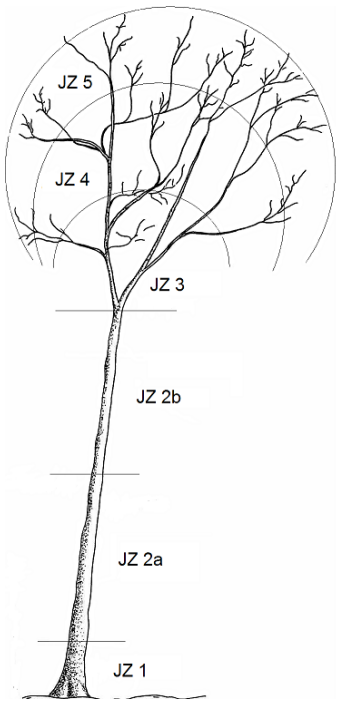

Fig 5.1: Illustration of the Johansson Zones (Johansson 1974). The zones include the base (JZ 1), lower trunk (JZ 2a), upper trunk (JZ 2b), inner canopy (JZ 3), mid canopy (JZ 4) and outer canopy (JZ 5). This figure shows the adapted version of the system, where the trunk is divided into two separate zones (ter Steege and Cornelissen 1989). Illustration adapted from Romanski et al. (2011).

5.3.2 Epiphyte sampling

We selected sites at 1000, 1090, and 1180 m above sea level (asl), on a south-western aspect close to the summit of Mt Lewis (1210 m asl). Here, the forest was protected from the prevailing south-easterly winds and tropical cyclones that are typical of this region (Adam 1994; McJannet et al. 2007). In this sheltered position, trees had an average height of 21 m (min.: 17 m; max.: 25 m), compared to the stunted forests that occur on the windward side of the peaks in this region. We sampled large canopy trees from two different bark categories—coarse (rough, hard bark) or fissured (rough, non-flaking bark with longitudinal grooves)—with five trees selected from each bark category at each site. Selected trees were at least 20 m apart and were chosen based on their suitability for climbing (healthy trees with large sturdy branches and no signs of rot). We recorded the height, species, exact elevation and location (GPS coordinates), and diameter at breast height (dbh, measured at 1.3 m from the ground) for each tree (see table 2.1). Average tree dbh was 51 cm (min.: 42 cm; max.: 66 cm). We climbed trees using a combination of single and double-rope climbing techniques (Lowman and Moffett 1993). We conducted fieldwork in July and August 2014.

Each tree was divided up into the Johansson zones (Fig. 1). These were the base (JZ 1; from the ground to 2 m), trunk (JZ 2; 2 m above the ground to the first bifurcation), inner canopy (JZ 3; the inner third of the branches in the crown), and the mid-canopy (JZ 4; the middle third branches of the crown). We chose not to survey the outer canopy (JZ 5; the outer third of the branches of the crown) as this zone is difficult to safely access and to reach the epiphytes *in situ*. We also chose to divide the Johansson trunk zone into two equal zones: the lower and upper trunk (JZ 2a and JZ 2b, respectively). Previous authors have used this adaptation to the Johansson zones as the upper trunk often has a very different microclimate to the lower trunk (ter Steege and Cornelissen 1989; Gradstein et al. 2003; Sanger and Kirkpatrick 2015). On each tree, we surveyed all vascular epiphyte individuals, except those in the outer zone (JZ 5). We observed very few epiphytes growing in the outer canopy during the surveys.

We surveyed holo-epiphyte, primary hemi-epiphyte and nomadic vines. Holo-epiphytes are defined as epiphytes which have no connection to the ground for their entire lifecycle (Kelly 1985; Benzing 1990). Primary hemi-epiphytes, commonly stranglers, are plants that begin their lifecycle as true epiphytes but later send feeder roots down the trunk of the host tree and connect to the ground (Kress 1986, Benzing 1990). Nomadic vines (also known as secondary hemi-epiphytes) are semi-epiphytic climbers which are functionally similar to epiphytes, as their adventitious roots are often used for nutrient and water uptake and they occasionally lose their connection to the ground (Wallace 1981; Moffett 2000; Zotz 2013). We collected species that we were not able to identify in

the field and took them to the Australian Tropical Herbarium (CNS) for identification. Nomenclature follows the currently accepted species names in Australia as defined by the Australian Plant Census (Council of Heads of Australasian Herbaria 2015) and the Australian Orchid Name Index (Clements and Jones 2008).

For each individual epiphyte, we noted the Johansson zone (ter Steege and Cornelissen 1989) and measured habitat features: height from the ground (m), branch size (cm), substrate depth (mm), and light (%). Substrate was defined as any humus or bryophyte mats upon which the epiphyte was growing and was measured using a calliper directly beside the base of the epiphyte. For rhizomatous epiphytes, several measurements were taken and then averaged for the individual.

We measured light using hemispherical canopy photography, a method widely used to calculate transmitted light for a particular point within a forest (Frazer et al. 1999). We used a Cannon 5D mark III digital camera (Ohta-ku, Tokyo, Japan) with a Rokinon 8 mm f/3.5 HD fisheye lens (Gangnamgu, Seoul, Korea) to take hemispherical photographs 30 cm above each individual epiphyte. Results are optimal when photographs are taken on uniformly overcast conditions to remove the effect of direct solar irradiance; however, this was unachievable due to variable weather conditions and limited time in the field. To control for variations in sunlight, we took all photographs in manual mode with adjusted shutter speed and aperture to best suit light conditions. Using Photoshop (Adobe, San Jose, California, USA), the light levels were balanced using a standardized histogram reference, and clarity and edge sharpness was applied to each photograph. This helps to standardize the photographs and to reduce highlights from around the edge of leaves. We then analyzed photographs using Gap Light Analyzer (Frazer et al. 1999) which calculates the percentage of total transmitted light for each image over an entire year by transforming the image pixel positions into angular coordinates (Frazer et al. 1999).

5.3.3 Data analysis

We used a permutational analysis of variance (PERMANOVA) to test for any effects of site or bark type on the species composition of epiphytes. To assess the similarities in realized niches, we placed epiphyte species into groups using cluster analysis. Only species which had frequencies over ten and individuals recorded on at least three trees were included in ordination and classification analyses. We used a principal component analysis to ordinate the species by habitat, based on their median values for light, height, branch size, and substrate depth. Most of the variables were not normally distributed making the median value appropriate. We used the species scores on the first three components (cumulative eigenvalue: 0.978, Table 5.1) to create a Euclidean distance matrix. Ward's

Table 5.1: The cumulative eigenvalues across the three principal components and the weightings for each microhabitat variable for each of the three principal components.

Variable	PC1	PC2	PC3
Cumulative eigenvalue	0.799	0.937	0.978
Height	0.542	0.019	0.035
Branch size	0.514	0.319	0.740
Substrate	0.431	0.849	0.053
Light	0.506	0.421	0.670

method for agglomerative cluster analysis (Ward 1963) was used on the Euclidean distance matrix to create groups of species (Fig. 2). We chose four groups as the closest approximation to the number of Johansson zones studied, as the five group solution included a group with only two species and the six group solution contained a group with one species and a group with two species (Fig. 2). Plots of the distribution of species on the first three principal component axes were created to validate the groups selected from the dendrogram. Vectors for the environmental variables were fitted to the three dimensional ordination space.

The groups created by the cluster analysis were tested for differences in the median light, height, branch size, and substrate depth using Kruskal-Wallis tests. Mann-Whitney U-tests were used to test for differences between medians for pairwise comparisons. Chi-square test for association was used to test for differences in distributions of the groups over the five Johansson zones. Expected values were calculated from the number of individual epiphytes within each group (Group 1: 219; Group 2: 253; Group 3: 398; Group 4: 341) times by the distribution of epiphytes across the height zones (base: 12%; lower trunk: 9%; upper trunk: 13%; inner canopy: 48%; mid-canopy: 18%). The PCA, cluster analysis, Kruskal-Wallis tests, Mann-Whitney U-tests, and chi-square tests were completed in Minitab 16.1.0 (Minitab, Philadelphia, USA). The PERMANOVA was completed in Primer v.6 with PERMANOVA+ add-on software (Primer-E Ltd, Plymouth, UK). PCA plots and vector fitting were completed using the procedure in Primer v.6.

5.4 Results

A total of 1211 individual epiphytes were surveyed, belonging to 42 species. Only 24 species (1155 individuals) had abundances greater than ten and were found on three or more host trees. Eleven of the species were ferns, five species were orchids, and eight species were dicotyledonous plants. Seventeen species were holo-epiphytes, six were nomadic vines, and one was a primary hemi-

epiphyte. There was no effect of site (PERMANOVA; Pseudo-F: 1.3; P = 0.16) or bark type (PERMANOVA; Pseudo- F: 1.39; P = 0.173) on epiphyte species composition.

Group 1 contained six species, with an even mix of ferns and dicots. All species were holo-epiphytes except for one species of nomadic vine. Group 2 was the largest group with eight species and had five species of fern, two species of orchids and one dicot, which were all holo-epiphytes, except for one dicot hemi-epiphyte. Group 3 had four species in total, three orchids and one species of fern, all holo-epiphytes. Group 4 had six species, which were all nomadic vines except for one holo-epiphytic fern. There were four dicots and two fern species in this group. The cluster analysis dendrogram (Fig. 5.2) and the PCA plot (Fig. 5.3) show a large dissimilarity in niche characteristics between Group 4 and the other three groups, although groups 1, 2, and 3 are also mutually distinct.

The species groups varied in their Johansson zone distribution (Chi^2: 837.4; P < 0.001; Table 5.2). Groups 1 and 2 had very similar distributions over the zones, with 65–66 percent of individuals occurring in the inner canopy, 17–18 percent in the mid-canopy, 11–14 percent in the upper trunk, and few individuals in the lower trunk and the base (Fig. 5.4). Group 3 had a similar number of individuals in the inner canopy (64%) and a higher than expected number of individuals in the mid-canopy (32%). Group 3 also had lower than expected distribution over the base and trunk, with few or no individuals in these zones (Fig. 5.4). Group 4 had the opposite pattern, with higher than expected abundances over the base and two trunk zones (25–38%) and fewer individuals than expected in the inner and mid-canopies (Fig. 5.4).

The median height above the ground differed for each group, with Group 3 occupying the highest sites (14.5 m), followed by Group 2 (13 m) then Group 1 (11.5 m), with Group 4 (3 m) having the lowest median height (H = 601.1; df = 3; P < 0.001; Fig. 5.5A). For light, each group was significantly different from the others, with Group 3 having the highest median light measurements (26.6%), followed by Group 1 (22.7%), then Group 2 (21.9%) and with Group 4 (13.9%) occupying the shadiest sites (H = 497.5; df = 3; P < 0.001; Fig. 5.5B). There were also significant differences in the median branch size of each group, with Group 4 (47 cm) occupying the largest and Group 3 the smallest (19 cm; H = 414.7; df = 3; P < 0.001; Fig. 5.5C). Groups differed significantly in median substrate thickness, with groups 2 and 3 growing on the thickest substrate (5.5 and 5 mm, respectively), followed by Group 1 (1 mm) and with Group 4 having the thinnest substrate (0.5 mm; H = 276.7 df = 3; P < 0.001; Fig. 5.5D).

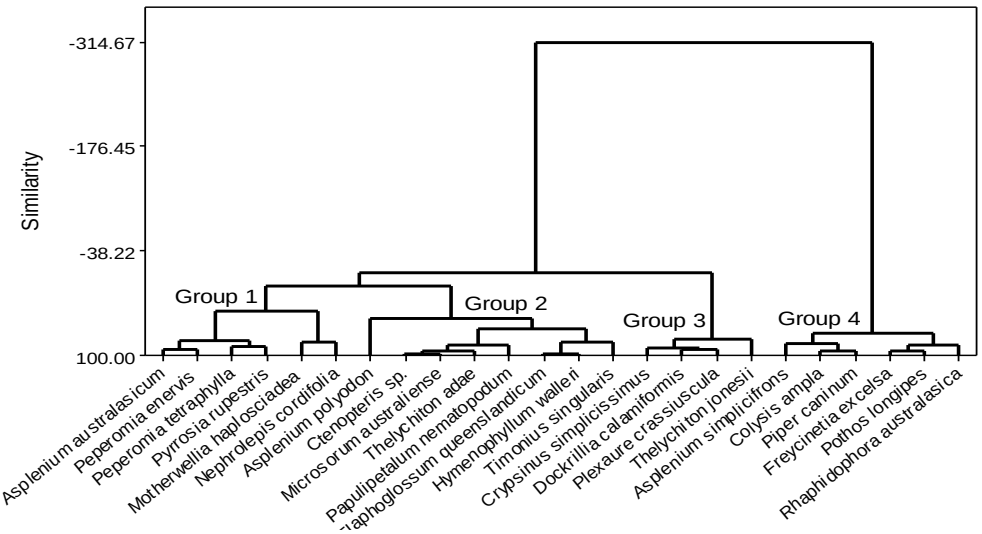

Fig 5.2: Dendrogram depicting the four niche groups. The clustering was computed using the Ward algorithm on Euclidean distance matrices of the PCA scores from the habitat variables light, height, branch size and substrate thickness.

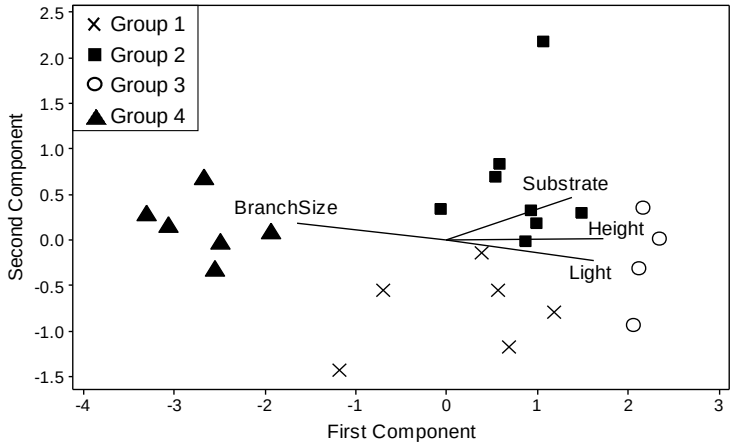

Fig 5.3: A bi-plot derived from the PCA showing the distributions of species across the first and second component. The bi-plot shows the four groups derived from the cluster analysis. Lines depict the direction and strength of the influence of the four habitat variables, height, light, substrate and branch size.

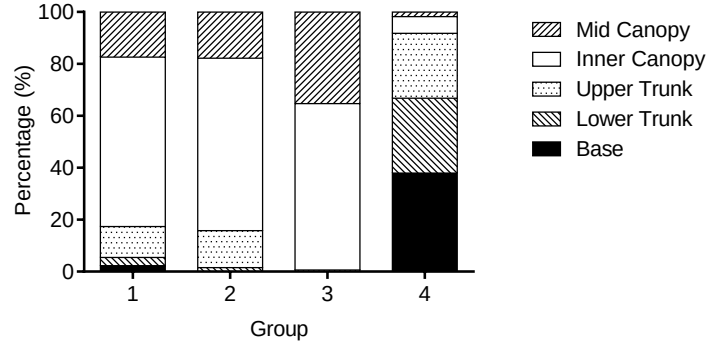

Fig 5.4: The distribution of species in each niche group over the five Johansson Zones.

Table 5.2: Results for the Chi^2 Test for Association to test for differences in the distribution of the species within the groups over the Johansson zones. The table shows the number of observed individuals (Obs), the

number of expected individuals (expected), each cells contribution to the overall Chi^2 statistic (Chi^2) and the P value for the individual cell (P value). Overall Chi^2 statistic was 837.35 ($P < 0.001$) with 12 degrees of freedom.

Group	Statistic	Base (JZ 1)	Lower Trunk (JZ 2a)	Upper Trunk (JZ 2b)	Inner Canopy (JZ 3)	Mid Canopy (JZ 4)
1	Obs.	5	7	26	143	38
	Expected	25.5	20.72	28.33	104.75	39.73
	Chi^2	16.47	9.09	0.19	13.97	0.08
	P value	NS	NS	NS	NS	NS
2	Obs.	0	4	36	168	45
	Expected	29.43	23.94	32.72	121.01	45.90
	Chi^2	29.43	16.61	0.33	18.25	0.02
	P value	0.003	NS	NS	NS	NS
3	Obs.	0	0	2	218	120
	Expected	39.55	32.17	43.98	162.62	61.68
	Chi^2	39.55	32.17	40.07	18.86	55.13
	P value	<0.001	0.001	<0.001	NS	<0.001
4	Obs.	129	98	85	22	6
	Expected	39.55	32.17	43.98	162.62	61.68
	Chi^2	202.32	134.71	38.27	121.60	50.27
	P value	<0.001	<0.001	<0.001	<0.001	<0.001

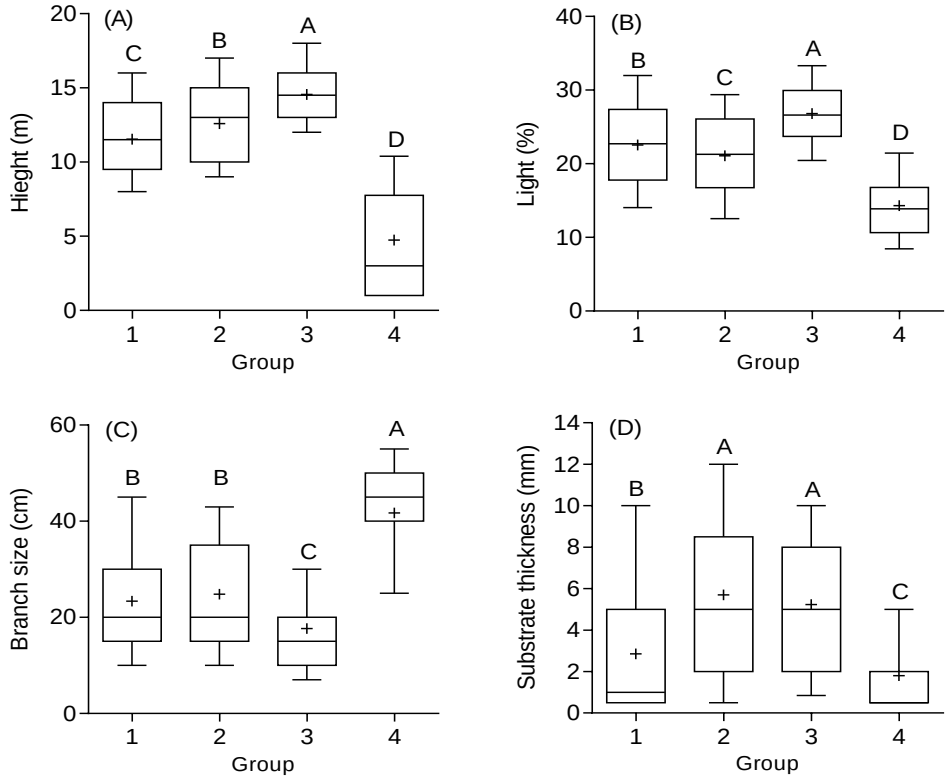

Fig 5.5: Differences the distributions of the four niche groups over (A) height from ground, (B) light, (C) branch size and (D) substrate thickness. Different letters signify significant differences (P < 0.05). The boxes represent the inter quartile range, the centre lines of the boxes represent the median, the crosses represent the mean and the whiskers extend from the quartiles to the minimum/maximum.

5.5 Discussion

The Johansson zones are a widely utilized system in epiphyte studies. Its simplicity allows for rapid and easy implementation in the field (Gradstein et al. 2003). Furthermore, its wide use provides easy comparison between trees and between different areas (Nieder and Zotz 1998); however, only for large trees within forests (Zotz 2007; Mendieta-Leiva and Zotz 2015). Previous authors have stated that it is the best method to use to study the spatial distribution of epiphytes until more developed spatial analysis tools become readily available (Nieder and Zotz 1998; Zotz 2007). Our study suggests that while some broad patterns of epiphyte associations do exist and fit loosely within the Johansson zones, the use of this system may mask some of the finer scale habitat partitioning within the host tree.

While the species in our study separated into distinct niche groups, the groups only partially matched with the individual Johansson zones. Groups often covered two to three adjacent zones, a phenomenon not uncommon in epiphyte communities (Wallace 1981; ter Steege and Cornelissen 1989; Kelly et al. 2004; Werner et al. 2005; Pos and Sleegers 2010). A study in the Bolivian Andes found that very few epiphytes are limited to one zone and that between 50 and 80 percent of vascular epiphyte species occur in most height zones (Krömer et al. 2007). There are also many examples in the literature that suggest that distinct epiphyte communities often span several zones (e.g., ter Steege and Cornelissen 1989; Kelly et al. 2004; Werner et al. 2005; Zotz 2007). For instance, three communities have been observed at the base/lower trunk (JZ 1 and 2a), upper trunk/inner canopy (JZ 2b and 3), and mid/outer crown (JZ 4 and 5) of trees in lowland rain forest of Guyana (ter Steege and Cornelissen 1989). A comparable distribution of epiphyte communities was observed in the montane rain forests in Ecuador (Bøgh 1992), the montane rain forests of Venezuela (Kelly et al. 2004), and lowland forests of Panama (Zotz 2007). A similar pattern has been found in our study, with Group 4 being the basal group, Groups 1 and 2 inner canopy groups and Group 3 the mid-canopy group. However, there was less distinction between the inner canopy and the mid-canopy groups in our study compared to elsewhere. This difference may have been more prominent if we included the outer canopy zone (JZ 5) in our study area. However, very few epiphytes were observed growing in the outer zone.

Despite the differences in microhabitat characteristics between groups 1 and 2, the two groups had close to identical distributions over the zones, with both having a strong association with the inner canopy (JZ 3). This suggests the coexistence of two different epiphyte communities, with Group 1 favouring lighter, more exposed habitats within the same vertical position as Group 2 in the host tree. The drier microclimate preference of Group 1 was further illustrated by the low level of

substrate associated with individuals from this group, as thick substrate can provide ongoing moisture to epiphytes between rain periods (Freiberg 1996; Nadkarni et al. 2004). The co-concentration of Groups 1 and 2 in the inner canopy may be due to its high microclimatic diversity due to differential shading by the thicker branches of the host tree (ter Steege and Cornelissen 1989; Cardelús and Chazdon 2005). The large branches of the inner canopy can provide suitable attachment sites for vascular epiphytes and bryophytes, which may be able to facilitate other vascular species (van Leerdam et al. 1990; Hietz et al. 2002). These factors create a patchwork of microhabitats within the same zone, allowing the two epiphyte communities to coexist. Many authors state that the accumulation of organic matter also influences the assemblage of epiphytes in the inner canopy (Nadkarni 1984; Ingram and Nadkarni 1993; Rudolph et al. 1998). At our study site, organic substrate rarely exceeded 20 mm at any point within the host trees, which contrasts with the thick moss mats and canopy soils that have been described in Neotropical cloud forests (Ingram and Nadkarni 1993; Nadkarni et al. 2004). Therefore, the canopy soils in our study may have less of an effect on epiphyte assemblages than those in other regions. However, the presence of canopy soils, even shallow substrates, is still influenced by the size and angle of branches, which adds further to the patchy mosaic of habitats for epiphytes (Ingram and Nadkarni 1993; Hietz and Hietz-Seifert 1995).

Many studies have found that there are distinct changes in species composition with microhabitat (ter Steege and Cornelissen 1989; Freiberg 1996; Cardelús and Chazdon 2005), with up to 57 percent of species showing microhabitat specialization (Woods et al. 2015). Our results suggest that microhabitats can constitute a patchy mosaic (Benzing 1995) within zones. If our study simply surveyed the trees using the Johansson zones, our conclusion would be that only three distinct epiphyte communities exist and that epiphytes have very broad distributions. However, our cluster analysis method has revealed that there were fine scale differences in the microhabitat preferences of epiphyte species within at least one zone.

The interpretation of the results of this study may have been influenced by the correlation among the variables. For instance, high light levels were correlated with small branch thickness. These correlations may have exacerbated differences of epiphyte species occupying the ends of the host tree gradient (Groups 3 and 4). Competition, facilitation, and dispersal also affect epiphyte distributions (Benzing 1990), which may account for some of the noisiness of our data. Some authors argue that dispersal limitations of epiphytes may lead to clumped distributions which can be mistaken for a preference for a certain microhabitat (Wolf 1994; Krömer et al. 2007; Ruiz-Cordova et al. 2014). Most Australian epiphytes are wind dispersed (Wallace 1981); therefore, dispersal

limitations may have affected the patterns within our study area. It is unlikely that competition has a strong influence on the epiphyte species distributions in Australian rain forests where individuals tend to be in low abundances (Wallace 1981). While bark type had no effect on the distribution of epiphytes within this study, there may be subtle differences between the host tree species that may have influenced the results. Differences in bark chemistry and other bark traits such as roughness and moisture holding content, which may not be uniform across the entire tree, may influence the distribution of epiphytes in this environment.

5.6 Conclusion

The epiphyte communities we observed are similar to those found in other parts of the world (e.g., ter Steege and Cornelissen 1989; Bøgh 1992; Kelly et al. 2004; Zotz 2007) in that there is a partial correspondence of their distributions with the Johansson zones. The Johansson zones describe epiphyte distributions well enough to be a useful descriptive framework and the wide use of the system gives the distinct advantage of easy comparison between different studies (Nieder and Zotz 1998; Zotz 2007). However, our work suggested that different epiphyte assemblages can exist within distinct environments in the same zone. Thus, the use of Johansson zones alone may obscure the finer scale effects of niche partitioning. We recommend that the Johansson zones are used in conjunction with other sampling methods which focus on smaller areas, especially in the inner canopy where there is a diversity of habitats.

Chapter 6

Conclusions

6.1 Main findings

The preceding chapters have shown that microclimate has a strong influence over epiphyte distributions within the Australian subtropical and tropical rainforest environment. Chapter 2 highlights how epiphytes show distinct patterns in distribution over two scales: within the host tree and across elevation. These two elements represent strong gradients of environmental factors such as moisture, temperature and light (Wallace 1981; Théry 2001; Chantanaorrapint 2010; Strong et al. 2011; Bartels and Chen 2012). Chapter 4 further illustrates how both host trees and elevation create strong gradients of moisture, with vascular epiphyte species with drought related morphologies and physiologies concentrated in drier habitats. Chapter 3 moved beyond the use of zones, which have been shown to have limitations (Chapter 5), by taking direct environmental measurements. These measurements highlighted how distributions of epiphytes are tightly linked with light and moisture, with differentiation between and within taxonomic groups.

The vascular epiphytes had similar patterns in distribution in both the subtropical and tropical sites. Orchids and species with drought-mitigating traits are common in the lower elevations and upper height zones, with ferns and less drought-adapted species occupying mid-elevations and lower height zones (Chapter 2, 4 and 5). Similarly, the orchids occupied the driest and sunniest ends of the environmental gradients, with ferns occupying a more mesic and mid light environment position on the gradient (Chapter 3). These patterns are similar to those observed elsewhere in the world (Wolf 1993; ter Steege and Cornelissen 1989; Freiberg 1996; Wolf and Flamenco 2003; Cardelús et al. 2006; Krömer et al. 2007; Cach-Pérez et al. 2013). Similarly, Chapter 4 has reinforced the generalisation that vascular epiphyte species have morphological and physiological characteristics that are congruent with habitat gradients in moisture and humidity (Pittendrigh 1948; Johansson 1974; Hietz and Briones 1998; Reyes-Garcia et al. 2012), however this pattern was less distinct in Chapter 3. The distribution of the epiphyte communities observed within the Johansson zones in Chapter 5 are also similar to those described in other parts of the world (eg. ter Steege and Cornelissen 1989, Bøgh 1992, Kelly et al. 2004, Zotz 2007) in that there is only a partial correspondence of their distributions with the Johansson zones, which are, nevertheless, a useful descriptive framework (Nieder and Zotz 1998, Zotz 2007).

Both moss and vascular epiphytes showed a distinct peak in species richness at mid-elevations (Chapter 2), which is a similar pattern to other regions of the world (Wolf 1993, 1994; Hietz and Hietz-Seifert 1995; Wolf and Flamenco 2003; Cardelús et al. 2006). As detailed in Chapter 2, most studies have examined the turnover of epiphyte species over much larger elevation gradients than the present study: 1550 m in Mexico (Hietz and Hietz-Seifert 1995); 1600 m in Spain (Caritat et al. 1997); 2570 m in Costa Rica (Cardelús et al. 2006); and 2420 m in the northern Andes (Wolf 1993; 1994). However, the 500 m tropical gradient and 900 m subtropical gradient studied in this thesis still showed noticeable differences in the species richness and composition of epiphytes. This is likely to be due to the cloud base typically sitting in the middle of both these transects (approx. 700 m at the subtropical site and 1000 m at the tropical site), creating distinct difference in moisture regimes between the lower and upper elevations (Wallace 1981).

Moss distribution within the host tree only had a partial fit to previously described patterns. Mosses had close to uniform species richness over the height gradient (Chapter 2) which differs from previous findings (Acebey et al. 2003; Sporn et al. 2010; Romanski et al. 2011; Silva and Pôrto 2013). Furthermore, the mosses often had distributions that seemed incongruent with their lifeform (Chapter 4). As shown in Chapter 5, there is not necessarily a continuous gradient of light and moisture with height in the host tree, with 'patchy mosaics' of potential microhabitats (Benzing 1995) complicating the vertical gradients. This patchiness in microhabitat may explain why many moss species had morphological characteristics that appeared inappropriate for the zones in which they occupied. Mosses, being smaller in size would have a much wider range of microhabitats available to them that are not accessible to large vascular species, such as between bark fissures or underneath a vascular epiphyte.

Host tree characteristics are often an important factor in influencing epiphyte distributions. Surprisingly, host tree characteristics had little to no influence over the composition of epiphytes within both the tropical and subtropical sites, which differs from the majority of studies conducted in rainforests outside Australia (ter Steege and Cornelissen 1989; Wolf 1993, 1994; Wolf and Flamenco 2003; Cardelús et al. 2006; Krömer et al. 2007; Zotz and Schultz 2008; Silva et al. 2010). While bark type had no influence on the distribution of epiphytes in this study, there may be other differences between the host tree species that may influence the results. For instance, there may be differences in bark chemistry and moisture holding content between tree species (Mehltreter et al. 2005). Other limitations or random variation may also have influenced the patterns observed in the present study. Limitations to dispersal have been suggested to play an important role in the distribution of epiphytes and some authors have suggested that clumped distributions may be more

of a result from limited dispersal than microclimatic conditions (Wolf 1994; Krömer et al. 2007; Ruiz-Cordova et al. 2014).

6.2 Implications of climate change

Considering the previous four chapters outline the tight coupling of epiphyte distributions with microclimate, it is very likely that epiphytes will be greatly affected by climate change (Benzing 1998; Hietz 1999; Foster 2001; Nadkarni and Solano 2002; Hsu et al. 2012). Detailed climatic modelling has predicted significant altitudinal shifts and often reductions in epiphyte species distributions. Hsu et al. (2012) assessed the impact of climate change on vascular epiphytes and associated forest types in Taiwan using species distribution models. They found that by 2100, 77–78% the of epiphyte species were projected to shift on average c. 400 m higher than current distributions and most species were estimated to lose 45–58% of their current range.

One of the biggest influences of climate change on epiphyte populations is likely to be from changes in rainfall and cloudiness. Both the subtropical and tropical rainforest regions in Australia are predicted to undergo a decrease in winter rainfall and a rise in temperature which may increase the elevation at which the cloud base settles (Still et al. 1999; CSIRO and Bureau of Meteorology 2015). The cloud base may lift up to hundreds of metres during the dry season in tropical montane forests, causing a reduction in low level cloudiness and an increase in the number of dry days (Pounds et al. 1999; Still et al. 1999; Foster 2001). These changes are likely to cause a corresponding shift in vegetation, with cloud forests predicted to being replaced by lower altitude ecosystems, both worldwide (Foster 2001) and in Australia (Laidlaw et al. 2011). Recent distribution modelling of Australia's Wet Tropics found that the future suitable climate niche of 19 high elevation plant species would reduce by an average of 81% by 2040 (Costion et. al. 2015).

The present thesis has shown that there are many epiphyte species in Australian rainforest which are drought sensitive, with several species inhabiting the wetter end of the moisture gradient or restricted to the upper elevations. Two filmy ferns, two orchid and five moss species have distributions restricted to above 900 m in the subtropical transect (Appendix 2). Similarly, one orchid, five fern, five other angiosperm species were only found above 1000 m on the tropical transect (Appendix 3). These species may be at risk of extinction under forecast climate change, especially species with limited dispersal which may not be able to reach new habitats. However, considering that the host tree is made up of a patchwork of difference microhabitats (Chapter 5), it may be possible epiphytes are able to migrate to a new, more suitable micro-habitat within their current geographical ranges. This may provide potential refugia for species that are unable to disperse long distances. Migrating to different microsites may potentially reduce biodiversity loss for

Australian cloud forest epiphytes, which are predicted to lose a substantial proportion of their habitat (Hilbert et al. 2001; ANU 2009).

Even relatively drought adapted species are still at risk from climate change, if drought periods increase in frequency and intensity over the next few decades as predicted (CSIRO and Bureau of Meteorology 2015). *Asplenium nidus*, the most common epiphyte in the lowland tropical areas of north-eastern Australia, can cope with low levels of rainfall during the dry season, however, high rates of mortality have been reported during longer than average dry periods (Freiberg and Turton 2007). High mortality rates of epiphyte seedlings and juveniles during intense drought periods have also been found several species throughout of the world (Zotz and Hietz 2001). Other factors associated with climate change such as host tree mortality, increased fire frequency and intensity, and increases in insects and pathogens could potentially further affect epiphyte populations (Bartels and Chen 2012).

6.3 Further research

There is still a lot to learn about how epiphyte species are distributed in the Australian environment. Understanding these distributions are important, especially considering the impacts of climate change. Australia may face a distinct reduction in cloud forest in the future, therefore epiphyte species with distributions at high elevations may lose their habitat. Microclimate may play an important role in helping at risk species persist in their geographical range. More studies need to focus on microclimates rather than just position or board sections in the host tree (such as the Johansson zones), as important details on microhabitat may be missed. The use of zonation systems is useful for comparisons with other regions or studies, however there are limitations to using these systems to classify epiphyte communities. A system which can easily incorporate habitat heterogeneity is needed.

More studies focusing on bryophytes, both in Australia and around the world, are needed. Cryptogams often make up a substantial proportion of overall diversity within a rainforest ecosystem (Cox and Larson 1993; Wolf 1994; Jarman and Kantvilas 1995; Cairns and Ramsay 2004), however there are a paucity of studies in tropical regions. Very little is known about the distributions of bryophytes in the Australian tropics and subtropics, with many species still remaining undescribed (Streimann 1994; Pócs and Streimann 2006).

Sufficient funding is currently a huge impediment for ecological research in Australia, not only for epiphytes, but for all biota. Over recent years, there has been a substantial drop in government funding for research programs in climate change, ecology and biodiversity. Sadly, many taxonomist

positions within government run herbaria have been lost, with taxonomists in 'unpopular' fields such as bryophytes often the first to go. Difficulties with taxonomy is one of the main reasons for the lack of studies into tropical bryophytes (Cox and Larson 1993) and losing our taxonomic experts only exacerbates this problem. We need a solid understanding of the distribution of Australia's epiphytes, especially our bryophytes, if we are to protect these species from climate change. If we are truly intending to conserve Australia's interesting and unique flora, including our wonderful and charismatic epiphytes, for future generations to enjoy, we need biodiversity conservation and climate change science to be made a priority.

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Appendix 2:

Species list and distribution of vascular and moss epiphyte species over the five elevations at the Border Ranges National Park, NSW.

	300 m	500 m	700 m	900 m	1100 m
Pteridophytes					
Aspleniaceae					
Asplenium australasicum **(J.Sm.) Hook.**	*	*	*	*	*
Asplenium polyodon **G.Forst.**	*	*	*	*	*
Davalliaceae					
Davallia solida **(G.Forst.) Sw.**	*	*	*	*	*
Hymenophyllaceae					
Crepidomanes vitiense **(Baker) Bostock**		*		*	
Hymenophyllum cupressiforme **Labill.**				*	
Hymenophyllum peltatum **(Poir.) Desv.**					*
Polypodiaceae					
Dictymia brownii **(Wikstr.) Copel.**	*	*	*	*	*
Grammitis billardierei **Willd.**			*		*
Microsorum scandens **(G.Forst.) Tindale**	*	*	*	*	*
Platycerium bifurcatum **(Cav.) C.Chr.**	*	*	*	*	
Platycerium superbum **de Jonch. & Hennipman**	*	*		*	
Pyrrosia confluens **(R.Br.) Ching**	*	*	*	*	
Pyrrosia rupestris **(R.Br.) Ching**	*	*	*	*	*
Psilotaceae					
Psilotum nudum **(L.) P.Beauv.**	*				
Pteridaceae					
Vittaria elongata **Sw.**		*	*		
Tectariaceae					
Arthropteris tenella **(G.Forst.) J.Sm. ex Hook.f.**		*		*	*
Arthropteris beckleri **(Hook.) Mett.**		*	*	*	
Angiosperms					
Araceae					
Pothos longipes **Schott**	*	*	*	*	*
Dioscoreaceae					
Dioscorea transversa **R.Br.**	*	*			
Moraceae					
Ficus watkinsiana **F.M.Bailey**		*			
Piperaceae					
Peperomia tetraphylla **Hook. & Arn.**	*	*	*	*	*
Orchidaceae					
Adelopetalum exiguum **(F.Muell.) D.L.Jones & M.A.Clem.**			*	*	*
Cestichis coelogynoides **(F.Muell.) D.L.Jones & M.A.Clem**		*	*	*	*
Dockrillia dolichophylla **(D.L.Jones & M.A.Clem.) M.A.Clem. & D.L.Jones**				*	*
Dockrillia fairfaxii **(F.Muell. & Fitzg.) Rauschert**	*	*	*		
Dockrillia mortii **(F.Muell.) Rauschert**			*		
Dockrillia pugioniformis **(A.Cunn.) Rauschert**		*	*	*	*
Oxysepala schilleriana **(Rchb.f.) D.L.Jones & M.A.Clem**	*	*			
Oxysepala shepherdii **(F.Muell.) D.L.Jones & M.A.Clem**			*		*
Rhinerrhiza divitiflora **(F.Muell. ex Benth.) Rupp**	*	*			
Tetrabaculum tetragonum **(A.Cunn.) M.A.Clem. & D.L.Jones**		*			
Thelychiton falcorostrus **(Fitzg.) M.A.Clem. & D.L.Jones**					*
Thelychiton gracilicaulis **(F.Muell.) M.A.Clem. & D.L.Jones**	*	*	*		*
Thelychiton speciosus **(Sm.) M.A.Clem. & D.L.Jones**	*	*	*	*	*
Bryophytes					
Braithwaiteaceae					
Braithwaitea sulcata **(Hook.) A.Jaeger**	*	*	*	*	*
Bryaceae					

Rosulabryum billarderii **(Schwägr.) J.R.*Sp*ence**		*			*
Dicranaceae					
Dicranoloma dicarpum **(Nees) Paris**		*		*	*
Dicranoloma leichhardtii **(Hampe) Watts & Whitel.**		*	*	*	*
Eucamptodon muelleri **Hampe & Müll.Hal.**	*	*	*	*	*
Holomitrium **perichaetiale (Hook.) Brid.**	*		*		
Fissidentaceae					
Fissidens **sp. Hedw.**			*		
Hypnodendraceae					
Bescherellia elegantissima **Duby**	*	*	*	*	*
Hypopterygiaceae					
Cyathophorum bulbosum **(Hedw.) Müll.Hal.**					*
Hypopterygium discolor **Mitt.**		*	*		
Lopidium concinnum **(Hook.) Wilson**			*	*	*
Lembophyllaceae					
Camptochaete excavata **(Taylor) A.Jaeger**	*	*	*	*	*
Camptochaete leichhardtii **(Hampe) Broth.**			*		
Leptostomataceae					
Leptostomum erectum **R.Br.**				*	*
Leucobryaceae					
Leucobryum **sp. Hampe**		*	*	*	*
Meteoriaceae					
Papillaria leuconeura **(Müll.Hal.) A.Jaeger**	*	*	*	*	*
Papillaria **sp. 2 (Müll.Hal.) Lorentz**		*	*	*	*
Papillaria **sp. 3 (Müll.Hal.) Lorentz**	*	*	*	*	*
Neckeraceae					
Thamnobryum pandum **(Hook.f. & Wilson) I.G.Stone & G.A.M.Scott**	*	*	*	*	*
Orthorrhynchiaceae					
Orthorrhynchium elegans **(Hook.f. & Wilson) Reichardt**			*		
Orthotrichaceae					
Macromitrium **sp. 1 Brid.**	*	*		*	*
Macromitrium **sp. 2 Brid.**		*	*	*	*
Macromitrium **sp. 3 Brid.**		*			*
Pterobryaceae					
Muellerobryum whiteleggei **(Broth.) M.Fleisch.**					*
Ptychomniaceae					
Ptychomnion aciculare **(Brid.) Mitt.**					*
Rhizogoniaceae					
Pyrrhobryum **sp. Mitt.**	*	*	*	*	*
Sematophyllaceae					
Sematophyllum **sp. Mitt.**	*	*			
Thuidiaceae					
Thuidium cymbifolium **(Dozy & Molk.) Dozy & Molk.**	*	*	*	*	*
Thuidiopsis sparsa **(Hook.f. & Wilson) Broth.**	*	*	*	*	*
Trachylomataceae					
Trachyloma planifolium **(Hedw.) Brid.**		*	*	*	*
Unidentified species					
Morphospecies 1	*	*	*	*	
Morphospecies 2	*	*	*	*	*
Morphospecies 3		*	*		*
Morphospecies 4	*	*	*	*	*
Morphospecies 5		*	*	*	*
Morphospecies 6				*	*
Morphospecies 7			*		*
Morphospecies 8		*	*		*
Morphospecies 9	*		*		
Morphospecies 10	*		*		
Morphospecies 11	*	*	*		
Morphospecies 12	*				

Appendix 3:

Species list and distribution of vascular epiphyte species over the five elevations at Mt Lewis, QLD.

	800 m	900 m	1000 m	1090 m	1180 m
Pteridophytes					
Aspleniaceae					
Asplenium australasicum **(J.Sm.) Hook.**		*	*	*	*
Asplenium polyodon **G.Forst.**		*	*	*	*
Asplenium simplicifrons **F.Muell.**	*	*	*	*	*
Davalliaceae					
Davallia solida **(G.Forst.) Sw.**	*				
Dryopteridaceae					
Elaphoglossum queenslandicum **S.B.Andrews**		*	*		
Hymenophyllaceae					
Hymenophyllum walleri **Maiden & Betche**		*	*	*	*
Lomariopsidaceae					
Nephrolepis cordifolia **(L.) C.Presl**			*		*
Lycopodiaceae					
Huperzia marsupiiformis **(D.L.Jones & B.Gray) Holub**					*
Huperzia phlegmaria **(L.) Rothm.**			*		
Ophioglossaceae					
Ophioglossum pendulum **L.**					*
Pteridaceae					
Monogramma acrocarpa **(Holttum) D.L.Jones**			*		
Polypodiaceae					
Belvisia mucronata **(Fee) Copel.**		*	*		
Colysis ampla **(F.Muell. ex Benth.) Copel.**		*	*	*	*
Ctenopteris sp. **Brongniart**		*			
Drynaria rigidula **(Sw.) Bedd.**	*	*			
Microsorum australiense **(F.M.Bailey) Bostock**			*	*	*
Goniophlebium subauriculatum **(Blume) C.Presl**		*			
Platycerium bifurcatum **(Cav.) C.Chr.**	*	*	*	*	
Pyrrosia longifolia **(Burm.f.) C.V.Morton**	*		*		
Pyrrosia rupestris **(R.Br.) Ching**				*	
Psilotaceae					
Psilotum complanatum **Sw.**		*			
Pteridaceae					
Vittaria ensiformis **Sw.**		*	*		
Tectariaceae					
Arthropteris tenella **(G.Forst.) J.Sm. ex Hook.f.**				*	
Arthropteris palisotii **(Desv.) Alston**				*	
Angiosperms					
Araceae					
Pothos longipes **Schott**	*	*	*	*	*
Rhaphidophora australasica **F.M.Bailey**	*	*	*	*	
Araliaceae					
Motherwellia haplosciadea **F.Muell.**			*	*	
Commelinaceae					
Crypsinus simplicissimus **(F.Muell.) S.B.Andrews**	*	*	*	*	*
Dioscoreaceae					
Dioscorea transversa **R.Br.**	*	*			
Ericaceae					
Paphia meiniana **(F.Muell.) Schltr.**					*
Moraceae					
Ficus triradiata **Corner**					*

Freycinetia excelsa **F.Muell.**	*	*	*	*	*
Piperaceae					
Peperomia tetraphylla **Hook. & Arn.**				*	*
Piper caninum **Blume**	*	*	*	*	*
Peperomia enervis **C.DC. & F.Muell.**			*	*	*
Orchidaceae					
Adelopetalum lageniforme **(F.M.Bailey) D.L.Jones & M.A.Clem.**		*	*		
Adelopetalum lilianiae **(Rendle) D.L.Jones & M.A.Clem.**		*			*
Adelopetalum newportii **(F.M.Bailey) D.L.Jones & M.A.Clem.**	*	*	*	*	
Bryobium queenslandicum **(T.E.Hunt) M.A.Clem. & D.L.Jones**	*				
Cymbidium madidum **Lindl.**	*				
Davejonesia prenticei **(F.Muell.) M.A.Clem.**	*	*			
Dockrillia calamiformis **(Lodd.) M.A.Clem. & D.L.Jones**		*	*	*	*
Oxysepala schilleriana **(Rchb.f.) D.L.Jones & M.A.Clem.**		*			
Papulipetalum nematopodum **(F.Muell.) M.A.Clem. & D.L.Jones**		*	*	*	
Plexaure crassiuscula **(Nicholls) M.A.Clem. & D.L.Jones**	*	*	*		*
Serpenticaulis johnsonii **(T.E.Hunt) M.A.Clem. & D.L.Jones**	*	*			
Tetrabaculum cacatua **(M.A.Clem. & D.L.Jones) M.A.Clem. & D.L.Jones**			*		
Thelychiton adae **(F.M.Bailey) M.A.Clem. & D.L.Jones**	*	*	*	*	*
Thelychiton jonesii **(Rendle) M.A.Clem. & D.L.Jones**	*	*	*	*	*
Thelychiton nitidus **(F.M.Bailey) M.A.Clem. & D.L.Jones**				*	
Trachyrhizum agrostophylla **(F.Muell.) Rauschert**		*			
Rubiaceae					
Timonius singularis **(F.Muell.) L.S.Sm.**	*	*	*	*	*

Appendix 4:

A list of the six groups of species with similar distributions. The table also shows the family, the frequency of species occurrence in the height zones, the taxonomic and life form group, the photosynthetic pathway, and any other drought mitigating morphologies. Carbon isotope ratios (‰) as described by Winter et al. (1983) have been added were applicable.

Species	Family	Freq.	Taxonomic group	Life form	Photo-synthetic pathway	Other morph-ology
Group 1 - Lower height zones, all elevations						
Arthropteris tenella (G.Forst.) J.Sm. ex Hook.f.	Nephrolepidaceae	11	Vascular	Nomadic vine	Unknown	None
Arthropteris beckleri (Hook.) Mett.	Nephrolepidaceae	4	Vascular	Nomadic vine	Unknown	None
Bescherellia elegantissima Duby	Hypnodendraceae	42	Moss	Dendroid	C_3	None
Camptochaete excavata (Taylor) A.Jaeger	Lembophyllaceae	55	Moss	Weft	C_3	None
Crepidomanes vitiense (Baker) Bostock	Hymenophyllaceae	3	Vascular	Filmy fern	Likely to be C_3*	None
Dioscorea transversa R.Br.	Dioscoreaceae	7	Vascular	Nomadic vine	Unknown	None
Fissidens sp. Hedw.	Fissidentaceae	1	Moss	Dendroid	C_3	None
Moss morphospecies 1	Unknown	18	Moss	Mat	C_3	None
Moss morphospecies 3	Unknown	6	Moss	Dendroid	C_3	None
Orthorrhynchium elegans (Hook.f. & Wilson)	Orthorrhynchiaceae	1	Moss	Mat	C_3	None
Phymatosorus scandens (G.Forst.) Tindale	Polypodiaceae	54	Vascular	Nomadic vine	Unknown	None
Pothos longipes Schott	Araceae	84	Vascular	Nomadic vine	C_3 (- 33.6 ‰)	None
Thamnobryum pandum (Hook.f. & Wilson) I.G.Stone & G.A.M.Scott	Neckeraceae	26	Moss	Dendroid	C_3	None
Thuidium cymbifolium (Dozy & Molk.) Dozy & Molk.	Thuidiaceae	46	Moss	Mat	C_3	None
Group 2 - Upper height zones, lower elevations						
Braithwaitea sulcata (Hook.) A.Jaeger	Braithwaiteaceae	58	Moss	Dendroid	C_3	None
Bulbophyllum schillerianum Rchb.f.	Orchidaceae	2	Vascular	Holo-epiphyte	CAM (-12.4 ‰)	Thick, leathery leaves
Dendrobium fairfaxii F.Muell. ex Fitzg	Orchidaceae	15	Vascular	Holo-epiphyte	CAM (-15.8 to -15.9 ‰)	Thick, leathery leaves
Dendrobium gracilicaule F.Muell.	Orchidaceae	12	Vascular	Holo-epiphyte	Weak CAM (-18.3 to 25.2 ‰)	Pseudobulb
Dendrobium mortii F.Muell.	Orchidaceae	1	Vascular	Holo-epiphyte	Unknown	Thick, leathery leaves
Dendrobium tetragonum A.Cunn. ex Lindl.	Orchidaceae	10	Vascular	Holo-epiphyte	CAM (-15.7 to -18.2 ‰)	Pseudobulb
Ficus watkinsiana F.M.Bailey	Moraceae	1	Vascular	Primary hemi-epiphyte	Unknown	Thick, glossy leaves
Moss morphospecies 11	Unknown	3	Moss	Mat	C_3	None
Papillaria sp. 2 (Müll.Hal.)	Meteoriaceae	37	Moss	Pendant	C_3	None

Lorentz						
Platycerium bifurcatum (Cav.) C.Chr.	Polypodiaceae	21	Vascular	Holo-epiphyte	C_3 (-24.9 to -25.1 ‰)**	Basket forming
Platycerium superbum Jonch. & Hennipman	Polypodiaceae	4	Vascular	Holo-epiphyte	C_3 (-22.8 ‰)**	Basket forming
Pyrrosia confluens (R.Br.) Ching	Polypodiaceae	72	Vascular	Holo-epiphyte	Weak CAM (-17.3 to 20.1 ‰)	Thick, leathery leaves
Psilotum nudum (L.) P.Beauv.	Psilotaceae	1	Vascular	Holo-epiphyte	Unknown	Thick, reduced leaves
Rhinerrhiza divitiflora (F.Muell. ex Benth.) Rupp	Orchidaceae	3	Vascular	Holo-epiphyte	CAM (-14.2 to 15.5 ‰)	Thick, leathery leaves
Rosulabryum billarderii (Schwägr.) J.R.Spence	Bryaceae	7	Moss	Mat	C_3	None
Sematophyllum sp. Mitt.	Sematophyllaceae	2	Moss	Mat	C_3	None
Thuidiopsis sparsa (Hook.f. & Wilson) Broth.	Thuidiaceae	50	Moss	Mat	C_3	None
Bulbophyllum exiguum F.Muell.	Orchidaceae	13	Vascular	Holo-epiphyte	C_3 (-26.2‰)	Pseudobulb, leathery leaves
Bulbophyllum shepherdii (F.Muell.) Rchb.f.	Orchidaceae	5	Vascular	Holo-epiphyte	CAM (-12.1 to -13.9 ‰)	Thick leaves, pseudobulb
Camptochaete leichardtii Brotherus	Lembophyllaceae	7	Moss	Weft	C_3	None
Holomitrium perichaetiale (Hook.) Brid.	Dicranaceae	4	Moss	Tuft	C_3	None
Lopidium concinnum (Hook.) Wilson	Hypopterygiaceae	16	Moss	Dendroid	C_3	None
Moss morphospecies 4	Unknown	33	Moss	Mat	C_3	None
Moss morphospecies 9	Unknown	10	Moss	Pendant	C_3	None
Moss morphospecies 10	Unknown	8	Moss	Dendroid	C_3	None
Moss morphospecies 12	Unknown	2	Moss	Mat	C_3	None
Papillaria sp. 3 (Müll.Hal.) Lorentz	Meteoriaceae	46	Moss	Pendant	C_3	None
Dendrobium dolichophyllum D.L.Jones & M.A.Clem.	Orchidaceae	4	Vascular	Holo-epiphyte	CAM (-15.8 to -15.9 ‰)	Thick leathery leaves
Dendrobium falcorostrum Fitzg.	Orchidaceae	7	Vascular	Holo-epiphyte	unknown	Thick leaves, pseudobulb
Dendrobium pugioniforme A.Cunn. ex Lindl.	Orchidaceae	43	Vascular	Holo-epiphyte	CAM (-13.9 to -15.4 ‰)	Thick, leathery leaves
Eucamptodon muelleri Hampe & Müll.	Dicranaceae	28	Moss	Mat	C_3	None
Hymenophyllum peltatum (Poir.) Desv	Hymenophyllaceae	2	Vascular	Filmy fern	Likely to be C3*	None
Leptostomum erectum R.Br.	Leptostomataceae	11	Moss	Tuft	C_3	None
Liparis coelogynoides (F.Muell.) Benth.	Orchidaceae	4	Vascular	Holo-epiphyte	C_3 (-26.3 to -27.3 ‰)	Pseudobulb
Macromitrium sp. 1 Brid.	Orthotrichaceae	30	Moss	Tuft	C_3	None
Macromitrium sp. 2 Brid.	Orthotrichaceae	9	Moss	Tuft	C_3	None
Macromitrium sp. 3 Brid.	Orthotrichaceae	8	Moss	Tuft	C_3	None
Moss morphospecies 2	Unknown	103	Moss	Mat	C_3	None
Moss morphospecies 5	Unknown	6	Moss	Tuft	C_3	None
Moss morphospecies 8	Unknown	11	Moss	Mat	C_3	None

Muellerobryum whiteleggei (Broth.) M.Fleisch.	Pterobryaceae	1	Moss	Tuft	C_3	None
Papillaria leuconeura (Müll.Hal.) A.Jaeger	Meteoriaceae	36	Moss	Pendant	C_3	None
Ptychomnion aciculare (Brid.) Mitt.	Ptychomniaceae	5	Moss	Weft	C3	None
Cyathophorum bulbosum (Hedw.) Müll.Hal.	Hypopterygiaceae	1	Moss	Dendroid	C_3	None
Dicranoloma dicarpum (Nees) Paris	Dicranaceae	11	Moss	Tuft	C_3	None
Dicranoloma leichhardtii (Hampe) Watts & Whitel.	Dicranaceae	12	Moss	Tuft	C_3	None
Grammitis poeppigiana (Mett.) Pichi-Serm	Polypodiaceae	2	Vascular	Holo-epiphyte	Unknown	None
Hymenophyllum cupressiforme Labill.	Hymenophyllaceae	3	Vascular	Filmy fern	Likely to be C3*	None
Leucobryum sp. Hampe	Leucobryaceae	54	Moss	Tuft	C_3	None
Moss morphospecies 6	Unknown	6	Moss	Tuft	C_3	None
Moss morphospecies 7	Unknown	4	Moss	Tuft	C_3	None
Pyrrhobryum sp. Mitt.	Rhizogoniaceae	35	Moss	Tuft	C_3	None
Asplenium australasicum (J.Sm.) Hook.	Aspleniaceae	66	Vascular	Holo-epiphyte	C_3	Basket forming
Asplenium polyodon G.Forst.	Aspleniaceae	34	Vascular	Holo-epiphyte	C_3 (-30.1 ‰)	None
Davallia solida (G.Forst.) Sw.	Davalliaceae	22	Vascular	Holo-epiphyte	C_3	Glossy leaves
Dendrobium speciosum Sm.	Orchidaceae	14	Vascular	Holo-epiphyte	CAM (-14.5 to -15.9 ‰)	Thick leaves, pseudobulb
Dictymia brownii (Wikstr.) Copel.	Polypodiaceae	45	Vascular	Holo-epiphyte	C_3 (-29.9 ‰)	Glossy leaves
Haplopteris elongata (Sw.) E. H. Crane	Pteridaceae	21	Vascular	Holo-epiphyte	C_3 (-30.1 ‰)	None
Hypopterygium discolor Mitt.	Hypopterygiaceae	4	Moss	Dendroid	C_3	None
Peperomia tetraphylla Hook. & Arn.	Piperaceae	46	Vascular	Holo-epiphyte	C_3 (-29 to -29.9 ‰)	Thick, glossy leaves
Pyrrosia rupestris (R.Br.) Ching	Polypodiaceae	261	Vascular	Holo-epiphyte	C_3 (-23.9 to 29.1 ‰)	Thick, leathery leaves
Trachyloma planifolium (Hedw.) Brid.	Trachylomataceae	37	Moss	Dendroid	C_3	None

*No data found for these species but previous studies on filmy ferns (Hymenophyllaceae) have shown species to be C_3 (Zotz 2004: $\delta^{13}C$ value -33.4 ‰)

**Winter et al. (1983) found no CAM in the two *Platycerium* species, however Rut et al. (2008) found CAM in the cover leaves of *Platycerium bifurcatum* and weak CAM in the closely related *Platycerium veitchii* (Holtum and Winter 1999)